

**NEST-SITE LIMITATION, NEST PREHENSION, AND  
NEST SITE SELECTION IN A CAVITY-PRESTING BIRD COMMUNITY**

By

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Abstract of Dissertation Presented to the Graduate School  
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HOST-ATTYLLATION, HOST PREDATION, AND  
HOST SITE SELECTION IN A COTTON AGROECO-SYSTEM

By

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I studied the abundance, seasonal activity, and mating success of adult cotton bollworms (*Helicoverpa armigera*) in a pine forest dominated by 15-40 year-old slash pines (*Pinus taeda*) plantations in northeast Florida during 1995-1996. My research focused on two primary questions: (1) Are adult cotton bollworm populations limited by host-site availability? (2) Is adult age correlated with rate of sex pheromone?

In a controlled, replicated outdoor experiment, bollworm densities at pine plantations increased on 8 treated plots but remained unchanged or decreased on 4 control plots without tree hosts. Species such as the Green-Crowned Brilliant (*Myioborus viridis*) that deposited clutches measured by image were not only found where species such as the Common Grackle (*Quiscalus quiscula*) had settled but were apparently in their stage of maturation (> 10% wing muscle coverage and movement was not restricted). The large number of unoccupied pine trees (over three years older than

correlations) support the latter theory, yet no upper limit on the number of breeding birds in older nesting theories.

I measured 227 nests of 11 species of pipits, 5 species of warblers, 10 boreal songbirds, 10 Myiotheres members of 9 species were included in the Green-tailed Towhee (Oreothraupis spixi) and Green-tailed Towhee (Mimus swainsonii) (10%), West population by our studies (Chaplin 1993), southern Flying-sparrow (Acanthis cabaret) (1%), and other species were the most common cause of nest failure. Nest predators were in the study were much greater than those documented at other locations for similar cavity-nesting species. Contrary to previous life history studies, I found no significant differences in clutch size or daily nest survival rates between successful and non-successful. These life history relationships need further exploration across a range of sites.

I found a variety of evidence supporting the hypothesis that nest predation is negatively associated with cavity size. Nest success was greater in newly excavated cavities than in cavities that had been used the previous year. Egg deposition in new nests occurred during the second year of their availability, probably as a result of nest predators leaving the nest after a period of post-laying predation.

## CHAPTER 1 INTRODUCTION

### Background

Since the late 1990s, conversion of natural longleaf pine (*P. palustris*) forest to non-native plantations of slash pine (*P. elliottii*) and loblolly pine (*P. taeda*) has drastically reduced the coverage of longleaf forest throughout the southeastern United States. The longleaf pine ecosystem now covers no less than 3% of its original pre-Columbian range (Price 1998; Price 1999). In Florida, managed pine plantations managed for pulpwood have replaced most of the longleaf forest.

The biodiversity of birdlife lost consequent to the extensive coastal pine forests converted by these forest management practices (Brennan and Luskay 1987) cavity-nesting species have been especially affected. Fifty years ago, the woodpecker fauna in northern Florida was diverse, with the Red-headed Woodpecker (*Melanerpes erythrocephalus*) and Red-bellied Woodpecker (*Picoides borealis*) common across a range of plant communities (Carrick 1931). Today, though, these two species (the Red-bellied Woodpecker (*Melanerpes carolinus*)) are protection throughout southern Florida (Oliver and Petrie 1998; also see Appendix A).

Banding Bird Survey (BBS)-data indicate that many cavity-nesting species in Florida have experienced population declines in recent decades. Cox (1997) analyzed BBS-data from 1987-1997 and demonstrated that while 8 of 10 (80%) cavity-nesters

species were declining, only 8 of 65 (12%) non-socially-feeding species were declining ( $\chi^2 = 1.71$ , d.f. = 1,  $P = 0.197$ ). During the 1980s, population declines of the Eastern Bluebird (Sialia sialis) were more severe in Florida than in any other southern state (Brown and Drago 1990).

Population declines of cavity-entering birds have been attributed to habitat degradation caused by intensive forest management practices (Dale 1977, Jenkins 1980, Langston 1982), but little research has been done on the specific mechanisms that have these species. Southern pine plantations are typically young stands managed for short rotations, and standing dead trees (snags) may be identified as diameter to provide nesting sites for many cavity-entering birds. Moreover, McCosh et al. (1986) argued that short-pine plantations had the lowest densities of snags of any forest type in Florida.

Currently, intensive research and management in southern pine forests focus primarily on the endangered Red-cockaded Woodpecker and the eastern longleaf pine which abounds in snags. At the same time, however, density measures like cover provide these subtropical longleaf forests conditions to have a maximum capacity for other cavity-nesters. In their landmark monograph on cavity-entering Birds, Raphael and White (1984) concluded that the determination of reproductive success in relation to nest-site characteristics and other habitat features should be a wildlife-management priority. However, since two decades later, the type of information is still unknown and incomplete. Despite the adequacy of planted pine, nesting success rates between the representatives of southern pine plantations are unknown for almost all species of cavity-entering birds.

Most of our knowledge about cavity-nesting birds is based on one-line studies of Old World species. Biologists have only recently begun to conduct intensive field study of cavity-nesting birds in several countries on various questions about avian life history theory and conservation ecology (e.g., Izsák and Brinkley 1991; Izsák and Izsák 1992; Pansch et al. 1997). With this in mind, I conducted a comprehensive 3-year study of the ecology of cavity-nesting birds in coastal pinelands in northern Florida.

#### Study Site

Cape Charles, Virginia, sits atop a Florida Department of Military Affairs Army National Guard facility encompassing 10,000 ha in City County, Florida.

Pinelands at CCHB are currently in poor condition because of the conversion of most of the original pine savannas and scrublands to short pine plantations and many years of fire suppression (Pope and Tolosa 1991). In these respects, I believe they are not typical of pinelands in contemporary Florida.

#### Study Species

A variety of 17 species of cavity-nesting birds occur in the pinelands of northern Florida (see Table 1), although one is a transient species (Yellow bellied Sapsucker), one is relatively rare (Brewer Owl), and one is arguably a "local and temporary" visitor and not an obligate cavity nester (Carolina Wren). That leaves 11 cavity-nesting species that are potential breeders in nesting at pinelands on the CCHB study area. Several of these species were rare in CCHB plantations (see Appendix A).

Table 1-1: County nesting bird species occurring in portions of Citrus Ranching Training Site

Common name	Scientific name	Least <sup>a</sup>	Near <sup>b</sup>	None <sup>c</sup>
Wood Duck	<i>Aix sponsa</i>			
Red-shouldered Hawk	<i>Buteo lineatus pectoralis</i>	?	X	X
Barn Owl	<i>Tyto alba</i>		X	
Eastern Screech Owl	<i>Otus asio</i>			
Pileated Woodpecker	<i>Dendrocopos pileatus</i>		X	
Mountain Plover	<i>Charadrius montanus</i>		X	X
Barred Owl	<i>Mitchocygnus诧vus</i>			
Red-headed Woodpecker	<i>Mitchocygnus erythropygialis</i>		X	X
Red-cockaded Woodpecker	<i>Picoides borealis</i>	X	X	X
Rusty Blackbird	<i>Pelagicus rufescens</i>			?
Swainson's Warbler	<i>Pooecetes gramineus</i>			
Yellow-bellied Flycatcher <sup>d</sup>	<i>Sympetrum variegatum</i>			
Great Crested Flycatcher	<i>Muscicapa cristata</i>			?
Tulip Tanager	<i>Flavolaterix flavipes</i>			
Cassin's Cardinal	<i>Paroaria dominicana</i>			X
Brown-headed Nuthatch	<i>Sitta pusilla</i>			X
Carolina Wren	<i>Thryothorus ludovicianus</i>			
Brown Thrasher	<i>Turdus migratorius</i>			X

<sup>a</sup> Endangered or threatened species

<sup>b</sup> Species given high C-30 biological concern status scores by the Florida Fish and Wildlife Conservation Commission (McIlroy et al. 1999)

<sup>c</sup> Breeding Bird Survey data indicate statewide rather regional population decline (Crisler 1981; Pyley et al. 1999)

<sup>d</sup> Whitney, then not found in Florida

## Research Questions

One of the oldest questions of interest to both ecological and wildlife management is whether cavity-nesting bird populations are limited by the availability of nest cavities. Although a generally accepted answer, and the literature rarely has been studied effectively with manipulative experiments. Thus, I conducted a controlled, replicated experiment to test the movement limitation in Florida panther kittens. I discuss my findings in Chapter 2, with special focus on antipredator variation in nest-site behavior.

My focus on antipredator studies study over life histories and population dynamics, but in recent years there has been wider interest in a variety of issues (e.g., Miller 1995) including the extent that nest boxes might be safer than predators that natural sites. In Chapter 3, I test this hypothesis by comparing reproduction success of Great Crested Flycatchers (*Muscicapa cristata*) in nest boxes with those in tree cavities.

Although nest predation has become an important focus of research in avian ecology during the last decade, relatively little attention has been devoted towards cavity-nesting birds, in part, because of the difficulty in assessing and mitigating the impacts of nesters on suitable sites. In Chapter 4, I examine nesting success and nest predators, rates for a community of cavity-nesting birds, focusing on the differences between raptor-prey species and non-raptor-prey species. I evaluate several hypotheses for why nest predators are more vulnerable to nest predators than scavengers.

Finally, Chapter 5 integrates the outcomes of each chapter and identifies key areas for future research.

## CHAPTER 2 DO MINE EXTRUDED (MELT) RAILING DEVICES OF ECONOMIC CARRY HEATING REACT?

### Introduction

There have been efforts concentrated by the primary focus on testing the responses of secondary (i.e., non-explosive) safety mining tools (SCHM) (e.g., van Hassel et al. 1973; Thomas et al. 1978; Cody 1981). However, despite decades of research on carry-heating tools, most of the non-rate limitation hypotheses by comparative experiments, which include knowledge of technical conditions, adequate controls, and implications (Hassell 1979), are still very... In a memorandum, Hassell (1996) concluded that more attention for the rate-limit hypothesis in safety mining tools is recommended. Among studies that tested or substantiated rate limit the carry-heating tools, Neveson (1994) identified only 11 studies that included both control and pre- and post-manipulation data; of those 6, only 2 (Neveson and Kyberd 1972; Brown and Roble 1980) had replicate study prints. Other recent years, in previous tests of the non-rate limitation hypothesis, include lack of spatial independence of experimental and control plots (e.g., Bell and Parsons 1993; Deacong and Neveson 1993) and inadequate controls because of placement of study plots in favorable plant accumulation (e.g., Deak 1980). Inadequate experimental controls can result in apparent experimental effects open to alternative explanations such as temporal and spatial variation in labor quality. In summary, there have been few

unrelated services experience when the study design allowed overlapping interventions at the nests.

Died and alive hatching studies have been conducted on a small number of species inhabiting European forests, especially the Great Tit (*Parus major*) and the Pied Flycatcher (*Ficedula hypoleuca*). Controlled tree-hole experiments have not been undertaken with cavity nesting birds in pine forests of the southeastern United States. Individual predators or predators (predator density) are commonly considered to limit the availability of nest sites (usage) that provide nest sites for cavity nesters (McCracken et al. 1985; Jackson 1986), yet the same site limitation hypothesis has not been tested empirically. The primary objective of this study was to test the hypothesis that site availability limits the breeding densities of NCPs in pine forests in southern Florida.

## Methods

### Study Plot and Experimental Design

Twelve plots situated in 12 study plots, in slash pine/*Croton* alluvial vegetation at Camp Blanding Training Site, a Florida Army National Guard facility in northern Florida (Fig. 1A). Plot sizes were 11-40 ha-old even-aged slash that had grown unburned for more than three years. To control for variation in site productivity, I distributed study plots evenly between plots ("Bennett" sites and their "Yardell" sites). "Bennett" slashwood was densely packed and characterized by moderately to poorly drained soils and a dense shrub layer of gallberry (*Garrya elliptica*), saw palmetto (*Chamaerops humilis*), and coastal scrubland shrubs (Abrahamson and Hansen 1982). "Yardell" slashwood were moderately spaced and characterized by well-drained sandy



Figure 1-1. Location of Florida 10-tapir photodetector study plots at Camp Blanding Training Site, Clay County, Florida, 1993-1994.

and a patchy understory of turkey oak (*Quercus laevis*) saplings. Below the savanna tree plantations, the understorey was dominated by longleaf pine (Table 1) and had a ground cover of grassland grasses and herbs (Fig. 1). Within each study plot, I measured live vegetation at prior event census (Mason et al. 1997) and created maps > 10 cm diameter at basal height (DBH) or tree (Fig. 1). These records in develop stand profile for each plot (Table 2-1). Most maps were too small for measurement by compass rose, <2% of planted maps were >21 cm DBH (compass rose).

Study plots were of equal size (10 ha) and dimensions (350 m x 400 m) and situated as far as possible (typically >70 m) from roads and other openings. Study plots were broadly dispersed in savanna spatial configuration. The northernmost study plot was 1.1 km distant from the southernmost plot, and the westernmost study plot was 0.7 km distant from the easternmost plot (Fig. 2-1). Mean distances between study plots averaged 1.2 km (range 0.1–3.6 km). A strip of wetland forest separated the two study plots that were only 0.3 km apart.

After two years of treefall, full surveys to document stand conditions (1991–1993), I applied treatments randomly in a balanced design (Table 2-2). Prescribed burns were conducted on 1) bareplots plots and 2) unburnt plots during January–February 1991. Winter burns decreased leaf litter and caused temporary (< c. 10 g/m<sup>2</sup>) reductions in the length of shrubs and saplings but did not cause tree mortality. During the first month of March 1991 (> 1 month before the breeding census for all SCV species), I transplanted tree hosts to all of the burned plots and in 4 of the unburned plots. Survey 4 included

Table 3.1. Stand profiles of slash pine plantations in the Seminole County Housing Tract Site, Florida, summer 1991.

Forest type	n	Canopy height	Total basal area	Other basal area	Stems/ha <sup>a</sup>
		(m)	(m <sup>2</sup> /ha)	(m <sup>2</sup> /ha)	
Pineywoods	4	19.4 (0.9) <sup>b</sup>	30.8 (0.28)	0.3 (0.01)	211 (2.8)
Roseland	6	11.3 (1.1)	24.3 (0.16)	0.1 (0.01)	34.8 (2.7)

<sup>a</sup> Standing dead trees >10 cm diameter at breast height.

<sup>b</sup> Mean (SD).

Table 1.1. Experimental design and types of treatments. Treatments (D = no treatment, X = non-lethal added, Y = non-lethal added after control had been randomly applied within tree type)

Plot #	2001	2002	2003	2004
<b>Elmwood</b>				
1	Ø	Ø	Ø	Ø
2	Ø	Ø	Ø	Ø
3	Ø	Ø	X	X
4	Ø	Ø	X	X
5	Ø	Ø	Y	Y
6	Ø	Ø	Y	Y
<b>Lindell</b>				
7	Ø	Ø	Ø	Ø
8	Ø	Ø	Ø	Ø
9	Ø	Ø	X	X
10	Ø	Ø	X	X
11	Ø	Ø	Y	Y
12	Ø	Ø	Y	Y

plus nest) was based on results (Table 3.2). Two pairs of breeding bird surveys were conducted to assess the effects of tree cover (1991–1992).

### West Beach

I measured 100 nest boxes throughout entire island. I used average of diameter to approximate all species of SCMs, except shags which have a thick gizzard. Nest boxes defined as cavity floor diameter (0.1 to 0.9 m or 1.4 to 1.8 m), as the diameter of the entrance hole (0.8 cm or 0.1 m), and as floor height above ground (1.1 m or 4.1 m). On each nest box grid, I measured 10 nest boxes (1 per box). Nest intervals are randomized array. The nest box study area is balanced; I don't design box size (small vs. large) or hole size (narrow vs. wide) or box height (low vs. high). I placed all nest boxes with the entrance hole oriented east and by-woodland, because eastern or southeastern orientation are preferred by many cavity-nesting bird species (Cratser 1973; Paliokas 1976; Jenkins 1979; Kavallines and Kotsopoulos 1994).

I repeated the counts of each nest box once every 10–14 d during April–May and once every 14–21 d during June–July. As soon as I observed nesting activity in a nest box, I measured the nest box, especially at 3 d intervals. Nestled boxes were marked with an obvious orange ladder. For analysis of nest box use, a nesting attempt was defined as a nest where a single pair box (Scallop flying squirrel (*Glaucomys sabrinus*) and other small songbirds were not discouraged from using) was used, because I wanted to study criteria maintaining higher nest utilization conditions. Repaired nest sites were defined as those nest boxes in which flying squirrels were observed on ≥2 occasions within a season.

## Nest Searches and Nest Monitoring

I used standard methods (Matsuura and Douglas 1993) to search the 90.9 ha area around my study plots from early April through early July, 1994–1995. I conducted search effort among plots and day periods (early morning, late morning) to maintain comparable search effort among study plots. Open nests were located, with nest records being updated at 1-4 d intervals to assess nesting status (Matsuura and Douglas 1993, Ralph et al. 1993). (See Chapters 3–4 for detection techniques used for monitoring activity nests.)

## Estimation of Bird Detection

I used the distance point count method (Ralph et al. 1993, Wilson et al. 1993) to estimate densities of breeding birds in study plots. Distance point counts differ from distance point counts in that points are distributed relatively close together within a single plot or transect line, and count data within each plot are pooled for analysis (Ralph et al. 1993).

From point survey methods followed methods outlined by Ralph et al. (1993). transects were conducted within 2-hr time periods, no counts were made during rain. Big roosting areas, both were flying above the canopy were recorded separately from roosted within a flock with each roost counted if they were clustered together in no adjacent flock-within a flock. I conducted all point-count surveys to determine and observe this. I estimated 5-minute count period because 64% of the species in this system were detected within the first two minutes (Gospodar 1993), and a longer count period would increase the likelihood of double counting (Koenig and Pitelka 1981). Due

four plot sites in August 1991 and April 1992 measured the effective detection distance was 1.2m for most species, including all cavity-entering species. Accordingly, I established six 12m radius point-count plots in spaced 125 m apart within each plot. I recorded birds within the 12m fixed-radius separately from birds >12m from the observer (Dunn et al. 1988; Beling et al. 1992). Each point-count radius was sampled three times per year, at intervals of 20 weeks between 20 April and the second week of June.

#### Analysis of Experimental Effects

I pooled fixed radius point-count data during each visit to a study plot because each plot was considered an independent unit for analyses (Ralph et al. 1991). Within each plot, I used the maximum point count for each species for comparisons among plots, treatments, and years. Great data were not included in the analysis because of heterogeneity of resource-use between individuals and years. I analyzed experimental effects with a mixed model analysis of variance (ANOVA) utilizing generalized least squares estimation (PROC MIXED, SAS Institute 1997). The model included four terms, Treatment (Control vs. nest box vs. Insect vs. nest box), Year (1991 vs. modified), Time, and random plot effect. I modeled the differences in point data between pre-treatment years (1991, 1992) and post-treatment years (1993, 1994) by using the average of the two pre-treated years as a baseline (non-significant analyses indicated that pre-treated years did not differ). Post-treatment years were treated separately in the ANOVA because I wanted to determine if responses to treatments changed over time. Coefficients of the variance (Schoenfeld's Residual Covariance) indicated that a model including interaction terms (Treatment x Year, Treatment x Time) best described the data for each

species. The significant terms in the model, pairwise differences of least squares means (PROC MIXED), determined the relationships between variables.

## Results

### Plant Cover Survey

#### Effect of soil treatments on early seedling bird populations

Secondary cavity nesters. I observed 6 species of Second SCNs during field work pre-treatments. One Crested Flycatcher (*Dicaeum erythrorhynchos*), Tailed Flycatcher (*Muscicapa caerulea*), Crested Titmouse (*Trochocercus melanurus*), and Eastern Starling (*Sturnus vulgaris*).

For all SCN species combined, the mixed model ANOVA, interaction of Treatment was the only significant term ( $F = 7.17$ ,  $\text{df} = 2, 3$ ,  $P = 0.03$ ) reflecting the change in mean's between pre-treatment year (1993, 1994) and post-treatment year (1997, 1998). After contrasts were applied, SCNs increased on treated plots but decreased slightly on control plots (Fig. 1-2). In the two-year post treatment, differences of least square means indicated that mean (mean + SE) were significantly greater ( $P < 0.01$ ) in untreated plots with nest boxes (PUB) ( $0.3 \pm 0.7$ ) than in control plots (CP) ( $0.1 \pm 0.1$ ). Crested tit were significantly greater ( $P = 0.02$ ) in treated plots with nest boxes (BNB) ( $0.4 \pm 0.4$ ) than in control plots. SCNs didn't differ between NB plots and BNB plots.

The Treatment  $\times$  Year interaction term approached statistical significance in the mixed model ( $F = 2.18$ ,  $\text{df} = 2, 3$ ,  $P = 0.11$ ), reflecting the different rates at which SCNs responded to nest boxes on NB and BNB plots. On NB plots, SCNs increased at pre-

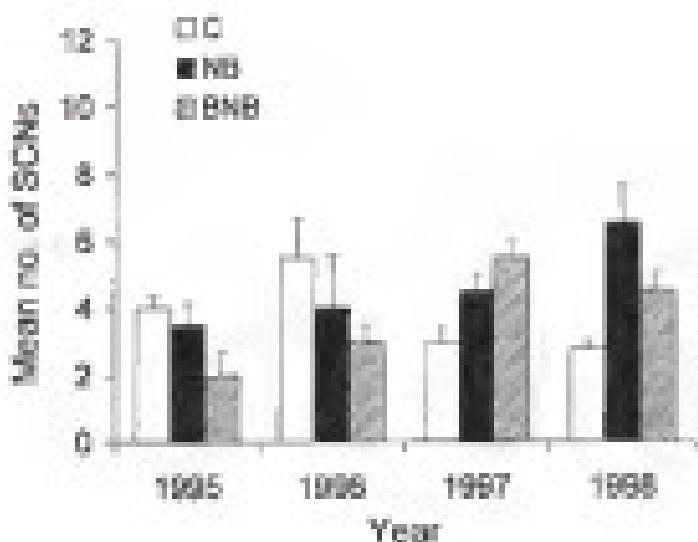


Figure 3.2. Mean density of secondary cavity borers (SCHEs) on plantation study plots (Bullock (1991-1992) and others (1991-1998) treatments (C = control; NB = untreated plots with seedlings; BNB = treated plots without leaves). Bars represent standard error.

treatment levels at 1991 and increased sharply in 1998 while on RSV plots SCWV exhibited no increasing trend in 1991 and decreased slightly during 1991 (Fig. 2-2). The largest increase in SCWV from one year to the next occurred in the first post-treatment year on RSV plots, when SCWV increased early twofold (Fig. 2-2).

**Primary cavity nesters.** I detected 8 species of primary (i.e., non-excavating) cavity nesters, including the Common Chimpanze (*Picus canus*), Brown-headed Nuthatch (*Sitta pusilla*), Red-bellied Woodpecker (*Melanerpes carolinus*), Red-headed Woodpecker (*M. erythrocephalus*), Downy Woodpecker (*Picoides pubescens*), Hairy woodpecker (*P. villosus*), Northern Flicker (*Cyanoptila cyanomelana*) and Pileated Woodpecker (*Dryocopus pileatus*). Although 4 species of woodpecker were reported, Red-bellied and Downy Woodpeckers accounted for 10% of all woodpecker-caused cavities [the ratios prior analysis]. Counts of primary cavity nesters did not vary among treatments, unless the all species combined ( $F^2 = 0.27$ ) or the very individual species ( $F^2 > 0.10$ ).

#### **Intraspecific variation in RSV response to tree felling treatments**

**Red Cross-billed Flycatchers.** Treatment was the only significant factor in the mixed model ANOVA ( $F^2 = 4.40$ ,  $\alpha^2 = 1.5$ ,  $P = 0.03$ ). After treatments were applied, Red Cross-billed Flycatchers increased on treated plots but decreased slightly on control plots (Fig. 2-1). In the first year post-treatment, counts in RSV plots ( $1.9 \pm 0.4$ ) were significantly greater ( $F^2 = 8.82$ ) than counts in control plots ( $0.3 \pm 0.3$ ), and counts in RSV plots ( $1.4 \pm 0.4$ ) were significantly greater ( $F^2 = 8.87$ ) than counts in control plots. MS plots and RSV plots did not differ. Least Cross-billed Flycatcher numbers reached their peak

during the study or the BVS plots during the first year after burns were introduced (Fig. 3-1).

The Tufted Titmouse exhibited a response to post-burns similar to that of the Chestnut-sided Warbler; mean increased diversity was mixed plots after treatments were applied (Fig. 3-4). Before and burns were introduced, Tufted Titmice were not recorded in basal-cover point counts on any BVS plots in 1990 and on only one BVS plot in 1991. However, Titmice was not significant in the mixed model ANOVA ( $F = 0.17$ ,  $df = 2, 5$ ,  $P = 0.93$ ), no doubt, largely because of the small samples involved. Tufted Titmice densities (Fig. 3-4) were reduced from all the Chestnut-sided Warblers (Fig. 3-1).

Carolina Wrens showed no response to treatments (Fig. 3-5). The Carolina Wren was the only SCW species that did not exhibit an immediate response to conditions on BVS plots in 1990. Forest was the only significant factor ( $F = 9.62$ ,  $df = 1, 5$ ,  $P = 0.01$ ) explaining the change in scores between pre- and post-treatment years. Not only were Carolina Wrens more common in Pinewoods plots than in Basal-Cover plots, but the difference in relative abundance between Forest types grew larger over time, regardless of treatments.

Eastern Bluebirds were either recorded on pinewoods study plots. No factors were significant in the mixed model ANOVA, although the small sample size precluded much in-depth analysis of differences. However, the fact that Bluebirds were not recorded in basal-cover point counts on any plots until after most burns were introduced (Fig. 3-4) strongly suggests that they responded to the post-burns.

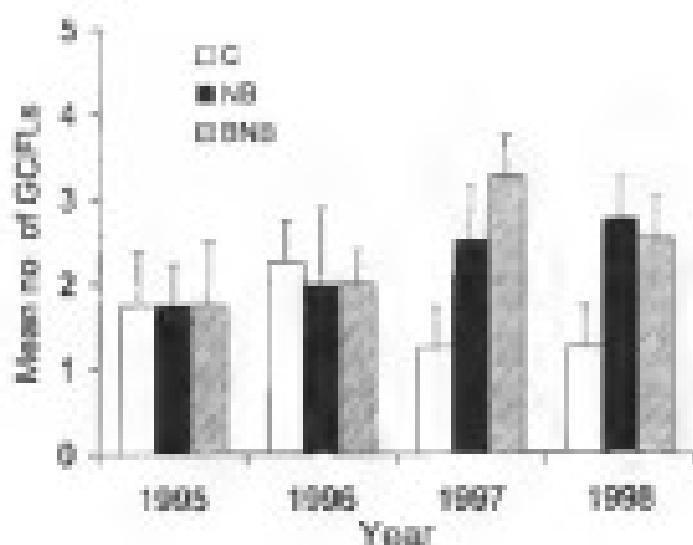


Figure 2. b. Mean counts of Geotomus Crassicornis (GCPLs) in plantation study plots (below 1100-1200 m and above 1200-1300 m elevation) (C = control; NB = untreated plots with red borer; BNB = treated plots with red borer). Data equal are treated borer.

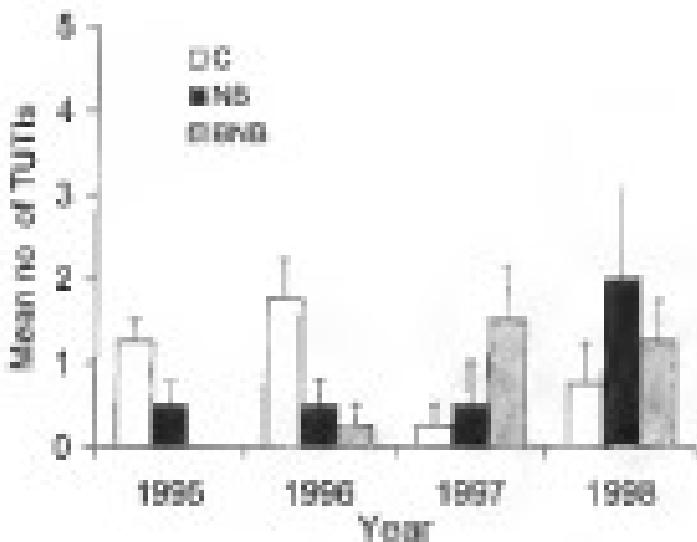


Figure 3.4. Mean counts of Tulip Tree (TULIP) tree plantation study plot index (1995-1998, and after 1998) treatments (C = control; MHS = untreated plots with tree holes; DMSO = treated plots with tree holes). Bars represent one standard error.

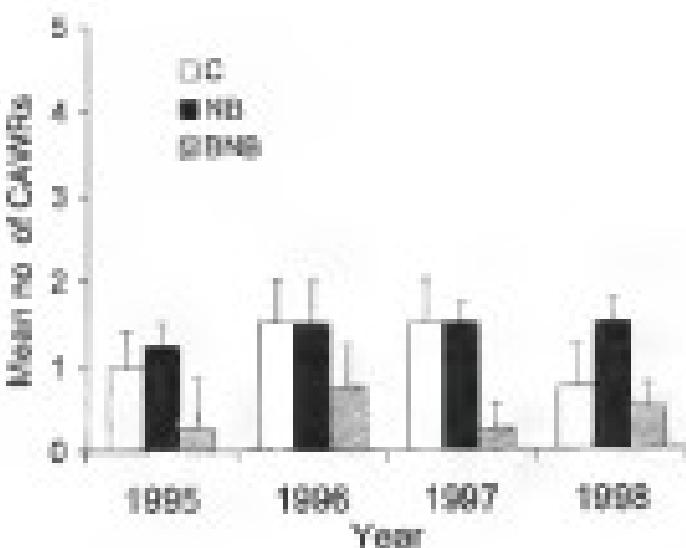


Figure 2.3. Mean counts of Carolina Wrens (CAVIRPs) in plantation study plots before (1995-1996) and after (1997-1998) treatments (C = control; NB = unbaited plots with natural bait; NBG = baited plots with natural bait). Bars equal one standard error.

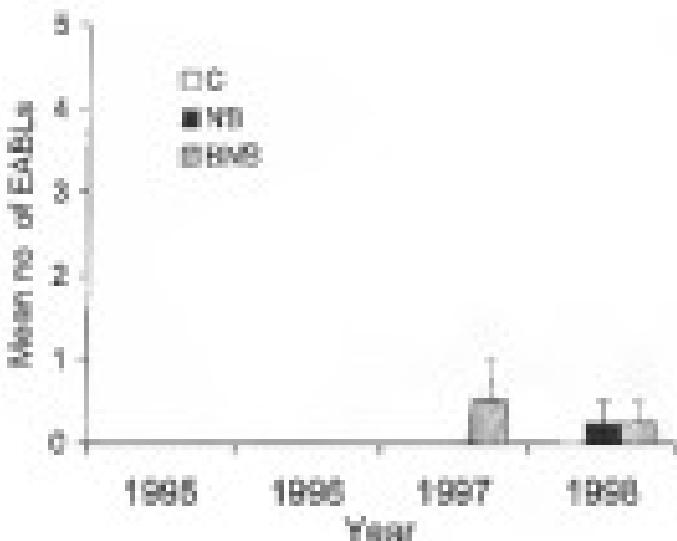


Figure 2d. Mean counts of Ecto-Parasitic Arthropods (EABLS) on *Phaseolus* study plots before (1996/1997) and after (1997/1998) treatments ( $N = 30$ ;  $\square$  - untreated plots with root knot, 1996;  $\blacksquare$  - treated plots with root knot;  $\blacksquare$  - treated plots root knot removed after)

## Post Monitoring

### Patterns of nest box occupancy

I recorded 17 nesting attempts in nest boxes during 1997–1998, including 11 (65%) Great Crested Flycatcher nests, 11 (65%) Buff-breasted Sandpiper nests, 4 (17%) Northern Shoveler nests, 3 (17%) Common Moorhen nests, and 1 (6%) Eurasian Bittern (Otorus europaeus) nest. Bittern chicks stayed only in nest boxes that had their entrance holes enlarged by spudgers. No non-spudger species nested in nest boxes. Nest Box Bellied Woodpeckers were observed using 17 nest boxes in replicated sites. Boxes used in replicated nests were positioned near and other food drifts and others were located >50 m from an active Bellied Woodpecker nest or a pair map. Overall mean occupancy of nest boxes, including woodpecker nest boxes, increased from the first year to the second year (P% and 15% in 1997 and 1998, respectively). SCW nests were built in 1% and 11% of the nest boxes in 1997 and 1998, respectively. Flying squirrels used nest boxes on all study plots, 70 (22%) and 54 (17%) nest boxes were used at most sites by flying squirrels in 1997 and 1998, respectively.

### Shore avifauna species versus nest boxes

The total number of SCW nests in study plots increased after nest boxes were introduced (Table 2–1). The total number of SCW nests (including Common Moorhen nests) increased twofold in 1997 (27 nest boxes) and decreased to threefold by 1998 (40 nest boxes) because of the large numbers of nesting attempts in nest boxes (Table 2–2). The relative abundance of SCW species was proportionately similar in quarry nests versus nest boxes. SCW density was approximately 10 times higher 1998–1999 included 19 Great Crested

Table 2.2. Mean of secondary cavity-making birds (Green Crested Flycatcher, Tailed Titmouse, Barren Warbler, Forest Flycatcher) based in tree cavities and in non-litter, fresh foliage (1980), and above (1982-1986) treatments applied. Control plots were not included because they caused only one nest.

	Incubation		Post-hatching, 1983	
	1980		1981	
	Occup. No.	Green	Occup. No.	Green
Control plots ( $n = 4$ )	0	— <sup>a</sup>	3	—
New litter plots ( $n = 4$ )	3	—	3	4
Fresh foliage plots ( $n = 4$ )	0	—	1	10
Total	11	—	7	14

<sup>a</sup> Nest never used available.

Type for now, 0 Tafford Threshers nests, 1 Eastern Shrike nest, and 1 Barn Swallow nest.

Net trap also indicated that nesting activity on NBL plots lagged behind those on DAB plots. NDN birds made their use of nest boxes on NBL plots until 1998 (the second year after the boxes were put on plots) (Table 3).

## Discussion

### Response Of Creeping-Passing Bird Populations To Plant Box Treatments

Plant box availability was a limiting factor on the breeding densities of NDN birds. Numbers of NDN birds recorded during the breeding season increased significantly on treated plots after nest boxes were installed. The number of NDN nesting attempts observed on control plots also increased several fold. Together, these data indicate that densities may be other supply before nest boxes were installed. Populations of insectivore species did not increase because they did not yet start breeding during the course of the study.

Decreases in NDN numbers are even more striking in light of the modest decreases that occurred annually on control plots (Fig. 3-2). Because control plots were not different from treated plots in tree density, tree age, or vegetation composition, the modest, yet non-experimental design suggests that NDNs would have declined on other plots if not treated with boxes. It is very unlikely that NDN birds moved from control plots to treated plots, because average distances were several times larger than the territory sizes of these species (Jain and Preestler 1994; Lanyon 1997; Corwin

and Phinney 1991). Even if some individuals did move between plots, the slight decline in number of cavity nests in control plots (plots A or B) in each of the fifteen years, Table 2-3) cannot account for the large increase in the number of total nests in treated plots during 1975-1990.

#### Intraspecific Variation in HCN Nesting by Species

Population responses to open burns by individual species ranged from moderately high (Great Crested Flycatcher) to low (Eastern Bluebird) in response of all (Carolina Wren). This does not probably account for interspecific differences observed in this study different levels of reliance on cavities increased in usage and difference in total population densities.

#### Great Crested Flycatcher

Great Crested Flycatchers responded more favorably to the addition of new burns to young plantations than did Eastern Bluebird and Eastern Kingbirds, suggesting that they probably were more cavity-discriminatory than the other two species. Similarly, Bush (1989) found that the migratory Ash-throated Flycatcher (*M. cinereiventris*) increased (from 0 to 1 breeding pair after 20 nest boxes were added to a 14-ha plot) of openings treated but non-treated of cavities. Walker et al. (1990) found no evidence of nest site limitation for Ash-throated Flycatchers at a mature oak-pine woodland with clusters cavities (nearly 3 per ha).

Nest site limitation in the Great Crested Flycatcher was probably related to its dependence on woodpecker-excavated cavities (nesting only 1 of the 11 (9%) cavity nests that I monitored were unexcavated except one long one (see also Chapter 4)).

Myrmecophytes can and do, not follow beetles and other large arthropods when they are available (pers. obs., Lanyon 1987), but such visitors did not exceed 10% of all plant visitors. Similarly, in a pine forest plot (*P. sylvestris*), 32% gnats did visit almost exclusively on personally unassisted visitors to plants (i.e., Visitor gnats (Horn, *Parthenomyia uliginosa*, *Pipunculus hirtipes*, *Ateles pumilio*, *Werneria flagellostoma*), Visitor gnats) exhibited greater population responses to 20% losses than those species that visited primarily in natural visitors and visitors (Elmes and Willis 1998).

#### Tufted Titmouse

The Tufted Titmouse increased in numbers following the introduction of nest boxes but not as dramatically as did the Chestnut Crested Flycatcher. The propensity of Tufted Titmice to visit a natural visitor is less than may partially explain why they did not respond to the nest box experiment as strongly as did Green Crested Flycatchers. Nest monitoring indicated that 1 of 6 (16%) tufted nests in chest pine were built at the natural visitors. Based between boxless pine trees (see also Chapter 8), The Tufted Titmouse's smaller body size may have allowed it to be more opportunistic in its use of natural visitors than the Chestnut Crested Flycatcher.

#### Carolina Wren

Carolina Wrens showed no response to treatments and, despite their abundance, nearly used nest boxes. Nest monitors indicated that Carolina Wrens typically built nests within side-polenated brush or low shrubs in brush piles, trees, and shrubs, making them less dependent on natural visitors than Tufted Titmice.

### **Eastern Blakely**

Eastern Blakely were as follows: these study plots had it is difficult to assess whether they were tree-line limited (although they did occur in very low numbers on four of the treated plots two years after tree-line was breached). The Eastern Blakely release on treeline-predator-mountain-tundra (Pielou 1979; see also Chapter 4) should result in tree-line limited, predator-free sufficiently extensive as suitable habitat. The plot as top site of tree-line limitation is the consequence of a minimum level of local recruitment of a given species at the study sites. For tree species, local or regional population densities are usually modified to provide the migration between individuals that would breed if more and more were available (Pielou 1979). Eastern Blakely populations have declined rapidly to Herds since the 1940s (Carr 1997, unpubl. data; Dugay 1998) and the species tree recruitment at the beginning of the study (two years after 1), perhaps because of many years of the suppression in Camp Blakely Training Site because the Eastern Blakely grows from edge and openings and older plant recruitment that offer low tree-cover ground cover (Dugay and Pielou 1998); these densely-tracked herb plots presumably may not agree with the site's structure (among Great Blue herds, Jones et al. 1999) occupied by Eastern Blakely.

### **Effect of Disturbance Intensity on Herb-site Limitation**

The degree of tree-line limitation for 10.2% did not vary between three types of herb on between glaciogenic and endoglacial plains responded similarly to treatments despite treated site differences in tree availability and densities (Table 2.1). Larger treatment differences between plant communities might have produced different results.

Regardless of forest type, the response to cut blocks was more rapid on forest plots. SCDs increased immediately on the forest plots with cut blocks, whereas SCD numbers on the uncutted (no) tree plots did not increase as rapidly until 1998, the second year after treatment (Fig. 3-1; Table 3-1). Population of many SCD species responded favorably to open microhabitats created by logging (e.g., Beck and Lynch 1979, Pollock et al. 1976, Bryant et al. 1984, Bentz 1991, Kettner and Bentz 1999). Lower discovery rates of cut blocks on PWD plots was probably the result of an atmospheric event, where winter rains had temporarily opened up the shrub layer and understorey.

#### Other Factors Potentially Limiting Crested-Wren Bird Populations

Residing populations of crested-wrens likely can be limited by other factors, including food, territoriality, and intraspecific competition for mates. The relatively low levels of nest box occupancy by birds (only 5% were used for nesting) could be indicative of low habitat quality (e.g., low food availability, unsuitable habitat structure). Other studies on southern forests have demonstrated a greater response to nest boxes. For example, at Russell prairie-gum forest in Arkansas, bird use of nest boxes increased from 12% on the first year of their availability to 50% on the fourth year (Bentz and Bentz 1991). Nest box occupancy rates on multiple woodlands in California increased from 20% on the first year to 60% in the ninth year (Pacek et al. 1997). In a nest box study of Bewick's Thrush (*Turdus bewickii*), Bryant (1984) found that population size did not increase until the third year after nest boxes were constructed. He attributed this to 2-year-old chicks, which were placed in new boxes during the first year.

amongst the breeding populations. It was unable to assess the impact of the additional year because of extensive tree cutting in several nest box plots during 1999–2000. However, I conducted monitoring diary plots that were unaffected by forestry operations and found that <1% of nest boxes were occupied by SCVs in the third and fourth year post-treatment. Thus, there is no evidence for continued occupancy in use of nest boxes until 2001.

I found little evidence that territorial or mateless-cooperation were important in this system. At present densities, territorial behaviour is unlikely to have been sufficient to prevent individuals from breeding. The multiple territory mapping (supplementary information) and Great-Crested Flycatcher territorial song activity analyses, which suggests that territorial behavior was not limiting, lend further support for this case. No significant difference between SCV species in territorial song activity, although I did observe several aggressive interactions between Red-bellied Woodpeckers and Great Crested Flycatchers at Red-bellied Woodpecker nest cavities (see also). The large number of nest boxes used by SCVs in these systems (approximately two-thirds of the total nest prey sites) suggested little potential for interspecific competition among species. I did not observe any interspecific cooperation of nest boxes, with the possible exception of two instances where flying squirrels and woodpeckers worked together at what appeared to be an incomplete nest box. In such cases, it was not determined whether the both had discovered their nest boxes after giving up occupation of the box by flying squirrels.

### Conclusion

Brown and Field's (1981) concluded that a given RCM population was 50%–60% located only if it was dependent on cavities generated by primary cavity-makers. Results of this study confirm the general species that were opportunistic or their absence at tree sites were less likely to exhibit population responses to the availability of tree holes. Two factors can play an interesting a particular species' reliance on cavities caused by secondary rot-holes: whether visual cavities (i.e., those not excavated by other birds) of a sufficient size are available, and whether tree-hole preferences are generalized enough to allow it to use the types of cavity-cavities and tree-hole availability the natural cavity-makers at given trees were apparently not sufficient nor for most Cross-Chested Flycatchers.

Nest-site location should not be measured for all cavity-making birds in all plant communities and locations. Whiteman et al. (1990) found no evidence that any RCM species was located by cavity availability in an oak-pine woodland in California that had abundant natural cavities. Brown and Field (1981) found that three RCM species were located by tree-hole availability in two open areas of ponderosa pine, but they based on evidence of tree-hole locations in a relatively dense, coniferous stand that contained more rocks and more snag. Natural cavities formed from decay are much more abundant in herbaceous than in woody (Whiteman et al. 1990) and tree-burrows and tree-logs are positively correlated with cavity-density (see Whiteman et al. 1990). Thus, it follows that RCM species are more likely to be located by tree sites in young forests and in forests dominated by snags.

The correlated view that services availability at the pasture fence limiting the breeding densities of SCW birds is an over-simplification. For example, Munro (1979, 1994) demonstrated that breeding densities of cavity nesting species can be limited by either food or space, or by both, depending on whether or not there is supply at a particular time and place. In my study, the large number of nestboxes and boxes (over three and a half years after they were installed) suggests that habitat quality may not be upper limit on the numbers of breeding birds in these pastures.

However, if these stock pine plantations are only marginally suitable as breeding habitats (i.e., for Eastern Bluebirds), then populations will not increase regardless of the number of crevices that become available. The immediate response of cavity nesters in non-hay plots that had recently been burned is consistent with the hypothesis that nest site limitation is mitigated by habitat creation (Brown and Dagle 1997). Subsequent prescribed burning over a period of years could enhance habitat quality for SCW, but long-term population effects of burning at regular intervals were outside the scope of this study. Prescribed burning seemed to facilitate the discovery and use of nest boxes by SCW in this study. If increasing cavity-nesting bird populations is a management goal in the maintained habitats, such as northern pine forests, managers may find that the addition of nest boxes to newly burned sites will result in the highest local densities of SCW birds.

CHAPTER 1  
MIXED SUCCESS OF THE GREAT CRESTED FlyCATCHER  
IN PROTECTED AREAS IN BRAZIL CAPTURED  
AND RELEASING SAFER FROM PREDATION

Introduction

Birds may not nest until they are two or three after they are mated. But it is the usual experience that one eventually finds a mate and develops a nest of eggs. Then either, a opportunity comes along or such is not.

— L. M. Linsley and C. G. Watson (1988) from "Breeding conditions in winter flocks," Transactions of North American Wildlife and Natural Resources Conference, 53:189-195.

Oncologists have used captrays to study cavity nesting birds for more than 70 years. Much of what is known about tree-hole nesting bird populations dynamics is based on data from field studies that use nest boxes. In recent years, the use of nest boxes as a research tool has been under criticism (Oliver 1983). Some have argued the new terms like "safe" descriptions that reflect nest rates and patterns of reproductive success observed in nest-box studies may be an artifact of nesting in boxes (Oliver 1984, 1986; Miller 1988; Freed et al. 1997). However, rigorous field tests of the assumption have been limited. Many studies that purport to show differences between nest boxes and tree cavities have compared reproductive parameters of separate populations at different locations (Lundberg and Alvarado 1997; Kishimoto and Alvarado 1997), while ignoring spatial and temporal differences in habitat quality and the density

of tree species. For example, Kullman and Ahola (1992) compared success of *Drimia Tenuissima* (Cochr.) Jucker in breeding at two sites in Finland over a 9-year period versus tree breeding in natural settings in Lithuania over a 27-year period. Two studies have compared nesting success of birds using nest boxes here and there in the same locality during the same time period.

Although some studies have found higher nesting success in nest boxes than in the savannas (Nilsson 1973, 1986; East and Pearce 1991), other studies have reported no differences between tree cavities and nest boxes (Kullman and Ahola 1992; Odeback 1993) or greater nesting success in cavity nests than in nest boxes (Jilg et al. 1992). However, when differences between tree holes and natural sites are found, they often do not occur for all cavity-nesting species within a particular study area (Nilsson 1986; Purcell et al. 1991). Within a given species, reproductive success can vary considerably over space and time because nest cavity g<sub>1</sub> for the European Starling, *Sturnus vulgaris* (Nilsson 1973, 1984, 1986; Karyendas 1986; Ahola et al. 1991; East and Pearce 1991), partitioning clutches proportionately about differences between nest boxes and natural tree holes.

Within a particular locality, nest boxes and tree cavities can differ at several respects that are typically not measured. Because nest height (Odeback 1984; Li and Blasius 1991) and incubation duration (Bellis, John, and Pearce 1991; Purcell 1991) can influence reproductive success in cavity-nesting birds, comparisons between nest boxes and tree cavities can be misleading if nest boxes are not placed at similar heights and in similar microhabitats.

My objective in this study was to compare nesting success of the Great Crested Flycatcher (*Muscicapa cretacea*) nest boxes and natural cavities in the same habitat during the same years. By analysis, measuring individual, 3-dimensional spatial and temporal factors in my comparisons, I also measured relationships characteristics of nest sites to verify the similarity of nest boxes and cavity nests and to assess the influence of these nest site characteristics on nest success.

## Methods

### Study Site and Study Species

I conducted my study in 25-40 yr-old slash pine (*Pinus elliotii*) plantations at Camp Blanding Training Site, a Florida Army National Guard Facility in northern Florida. My field experiments and I examined nests in tree cavities on twelve 10-ha pine plantation study plots, one 8-ha pine plantation study plot, and one 1.5-ha pine plantation that excluded small portions of turkey oaks (*Quercus laevis*). Eight of these study plots were instrumented with nest boxes. All 14 study plots were near aged pine slash banking to well developed undergrowth (see Chapter 7 for further description of the study plots). Density of nesting dead trees (snags) in these stands ranged from 1.7 to 19 per ha.

The Great Crested Flycatcher was the most common cavity-nesting avian species (i.e., non-migrant) species on the study area. A single-banded nesttopical migrant, it returns to the study area each year during the last week of March and begins breeding later in mid-to-late April.

### New Boxes

I constructed 160 new boxes of rough-cut cedar wood with no entrance hole (31 cm diameter) designed to accommodate Great Crested Flycatchers. Although the intrinsic behavior of different songbirds often vary by smaller species, including the Tüfted Titmouse (*Premnophilus familiaris*), Common Wren (*Troglodytes troglodytes*), and Eastern Bluetit (*Parus caeruleus*), the Great Crested Flycatcher was the only species that used new boxes in large numbers (see Chapter 2). I placed new boxes on eight more tree plots (30 per box per plot) during Primary March (1971–1980 work plots; I placed boxes on tree plots from all three intervals, alternating the heights at 1.8 m and 3.0 m above ground). All new boxes were mounted east by northeast, as is mostly or exclusively orientation in which preferred by many cavity-nesting bird species (e.g., Cresser 1973, Medilia 1978, McFarland 1992; Riedell and Riedell 1994). To minimize interplot differences among new boxes, I placed all new boxes where the scarce hole would not be observed by vegetation by >1.0 m in all directions (details below; formerly).

In a related study, 180 nest boxes with entrances too small (2.8 cm diameter) for the Great Crested Flycatcher were placed on the same study plots during Primary March (1971–1980) and largely were designed for the Tüfted Titmouse and Common Wren. Only 6 were used for nesting during (1971–1980).

### New Box Monitoring

I visited each nest box once every 10–14 d in April and May and twice every 14–21 d in June and early July. High nest boxes were reached with a telescopic extension ladder. As soon as I broadcasting activity by Great Crested Flycatchers in a nest box, I

measured the nest at 2-4 d intervals. I recorded all other species that occupied nests between Southern Flycatcher records (Glaucous, which were not evicted from nest boxes, because flycatchers and Glaucous Flycatchers naturally use the same nest tree location (p. 10), and I did not need to know the appearance of nesting individuals to make bird-level tree records). Because Flycatcher records are also potential nest predators, I counted all records observed in each nest box during monitoring visits to assess if Flycatcher densities changed over time as a result of the nest boxes. I defined primary nest sites as those nest boxes for which Flycatcher records were observed on two or more consecutive visited occasions.

#### Crabey Nest Monitoring

I used modified methods (Marxen and Gravel 1992) for nests by Cedar Crested Flycatchers were there and April through early July, 1993-1999. Nest census efforts included a full circle approximately 25m wide around each study plot to ensure that birds nesting in or near the edges of plantation plots also were monitored. I used non-invasive nest census plots and did patrols (early morning, late morning) to minimize unpairable search effort among sites. All birds in a nest were banded, or were measured regularly at 1-d intervals to assess nesting success (Marxen and Gravel 1992, Ralph et al. 1993). Nests located >25m above ground were reached with a step-ladder and the contents checked with a light and visual census to determine nest status. In 1997, nest contents photographs were taken from the ground through observation of which behavior (e.g., carrying nest material or food) was the cavity. Marxen and Gravel (1992, Ralph et al. 1993, Marxen et al. 1997), although more costly in longer-term stable surveys, were investigated

with the British standard brood-laying index. In 1995, all nestbox monitoring was associated with a voice probe mounted on a telecaching microphone (TeleCach, Sculpey Technologies Inc., Mission, California, USA). I considered nestlings to have fledged if they were observed outside within 1 h of expected fledging and subsequent observations showed no evidence of predation or disturbance to the nest (Marais et al. 1997). I recorded nestling fledge dates typically within 1–2 h after the expected time of fledging to ensure visual confirmation of the fledglings.

#### Statistical Analysis

Analyses of nesting success included data only from years in which at least one egg was laid. In analyses of nesting success by the Great Crested Flycatcher, I used 10% and 15% for the length of the incubation and nestling periods, respectively (Gospodinova, Teplova and Kurnikov 1991). The day the last egg was laid was considered the last day of incubation. For reasons that I could not suspect (i.e., some very high rates of infertility), I estimated the first day of incubation through observations of parental behavior at the nest (Marais and Ongpel 1997). I considered a nest to be successful if it produced >1 fledgling. I calculated nesting success rates with the Mayfield method (Mayfield 1961, 1963) as modified by Hensler and McNeely (1981). Nesting success rates for the incubation and nestling stages were calculated separately and then multiplied to determine overall success for the entire nesting period (Hensler and McNeely 1981, Hensler 1983). I tested for differences in nesting success between years and between nest types with two-tailed, standard paired *t* tests (Oehler and McNeely 1981, Hensler 1983).

I used a Wilcoxon signed rank test (ZII, 1993) to compare singing report numbers on study plots between 1997 and 1998. I tested for changes in (i) the number of nest boxes occupied by primary nest sites on each plot, and (ii) the maximum number of individuals present on nests in.

To determine if morphological differences existed between nest boxes among locations, I measured structural variables within circular plots centered on each nest. Within 3-m radius (9 m<sup>2</sup>) circular plots I measured percentage of bare ground, percentage of ground covered by grass, percentage of ground covered by shrubs, average shrub height, average pasture height, and number of epiphyte/green shrubs (0-2-4-6-8). Within 11.3-m radius (36 m<sup>2</sup>) circular plots, I measured the number of small trees (0-1-2-3), total basal area (m<sup>2</sup>/ha), canopy height, and maturity height. Methods for collecting data are similar to those of Martin et al. (1997). Heights of nest locations were measured with a clinometer. I used Kruskal-Wallis tests (Minitab Inc., 1996) to compare the heights of successful and unsuccessful nest sites and maturation index differences (MANOVDA) tests to compare morphological variables among nest sites. Variables recorded as percentages were  $(n-1)^2$  transformed before analysis.

## Results

### Singing Reports

During two breeding seasons, I monitored a total of 21-Dipod Capital Physotrichum nests at chick prior glorifications; 10 nests present 1997 and 21 nests in 1998 (Table 1). Most nest sites were at locations associated to song by the Bush-tit/White-throated

(*Molophilus maculatus*) or the Northern Flea (*Culicoides scutellaris*). In 6 (37%) cases no causal factors or reasons in living death place and ranking order.

Twenty-four of 29 cases (67%) presented at least one bedding. Overall May birth ranking scores were nearly identical between two years ( $0.167 \pm 0.032$ ) and two study sites ( $0.165 \pm 0.046$ ,  $F = 0.22$ ,  $P = 0.40$ ). However, differences were apparent when extremes of causal ranking scores were compared (Table 3-1). In 1991, ranking scores were higher in nest boxes ( $0.111$ ) than in aviaries ( $0.032$ ,  $F = 0.000$ ), whereas in 1998, ranking scores were lower in nest boxes ( $0.206$ ) than in aviaries ( $0.415$ ,  $F = 0.076$ ; Table 3-1). Within nest-box sites, ranking scores did not differ between years ( $F = 0.11$ ). Within nest boxes, ranking scores dropped from 53% in the first year to only 38% in the second year ( $F = 0.00$ ) due to fewer nest boxes during the population period (Table 3-1). I was unable to calculate the response for additional years because of substantial loss of nesting in several nest-box plots during 1998–2000.

Nest boxes that were used for a second time rated more highly in 1998 than nest boxes being used for the first time. One of the ten boxes used by Great Crested Flycatchers in 1998 had been previously used for nesting either by great tits or by Sedge Tits. Only 1 of these 6 (17%) were successful, while 5 of 14 (35%) nest boxes that had not had previous use were successful.

#### *Nest Predation*

Nest predation was the most common source of nest failure, representing the at least 28 of 59 (48%) nest failures. These were failed due to abandonment (due to pred-

Table 1-1. May-October mosquito rates of the West Coast Flavobacter in nest boxes and in tree cavities, Camp Blanding Training Area, 1993-1994.

	n	Mean mosquito (SE)	$\beta$
<b>1993</b>			
Nest boxes	13	0.331 (0.037)	-0.001
Tree cavities	10	0.332 (0.037)	
<b>1994</b>			
Nest boxes	10	0.700 (0.047)	+0.308
Tree cavities	17	0.405 (0.055)	

Practise in writing the following words and phrases in Hindi script.

Word	Script	Word	Script
स्वास्थ्य	स्वास्थ्य	विद्या	विद्या
स्वतंत्र	स्वतंत्र	विद्युत्	विद्युत्
स्वरूप	स्वरूप	विद्युतीय	विद्युतीय
स्वरूपी	स्वरूपी	विद्युतीयी	विद्युतीयी

Learn the following words and phrases in Hindi script.

from 2009 to 2010, and starting in 2010 to 2011, prior to cleaning the older nests, I was unable to determine nests of nest before the 1 week to lag time interval.

Documented nest predation of Great Crested Flycatchers included the nestling flying-squab and nest adult (laying) phases. Flying-squab preyed on 1 Great Crested Flycatcher nest during the incubation period. In such case, the eggs were broken or missing, the nest was in disarray, and flying-squab were observed on top of the nest, each of these nest predation events was documented only 1-2 d after the previous nest check. In addition, many depredated nests in nest boxes were destroyed in the field station during the incubation period but squabs were not subsequently observed. Care males preyed on 2 flycatcher nests, one containing five 10-day-old nestlings and the other containing three 10-day-old nestlings, no nest near the male remained in the box the two or more days after consuming the nestlings. Although yellow-race snakes (*Diaphorolepis aggregata*), were not observed preying on Great Crested Flycatcher nestlings during the study, they were known to prey on Red-backed Shrike nestlings in the study area (year 2010). Other potential, but not documented, nest predators in the study area included common rats (*Rattus rattus pacificus*) and Blue Jays (*Cyanocitta cristata*).

Despite the prevalence of flying-squab in nest boxes (see Chapter 2), I found no evidence that flying-squab populations increased during the course of the study. The total mean number of flying-squab created in each plot during the post-Great-Crested Flycatcher nesting season (mid-April through May) did not differ between years (Whitman signed rank test,  $P > 0.95$ ). The number of nest boxes occupied by flying-

species at primary tree sites during spring; and success rates did not differ between years (Wilcoxon signed rank test,  $P > 0.10$ ).

#### **Nest Mortality**

High and low nest losses were used by Dual Crested Flycatchers in similar proportions in 1997 and 1998 (Fisher's exact,  $P = 1.00$ ). The rate of successful to unsuccessful nests did not differ between high and low nest losses (Fisher's exact,  $P = 1.00$ ). Nest efficiency rates did not differ between years (Searle Wilks,  $\lambda = 0.97$ ,  $\chi^2 = 1$ ,  $P = 0.40$ ) or between successful and unsuccessful nests (Kruskal-Wallis,  $H = 0.01$ ,  $\chi^2 = 1$ ,  $P = 0.40$ ).

Morphological characteristics around nest sites did not differ between nest boxes and tree cavities (ANOVA, Wilks Lambda = 0.93,  $P = 0.22$ ). I found no evidence that nest boxes selected for nesting in 1998 differed from those selected in the previous year in morphological measures (ANOVA, Wilks Lambda = 0.98,  $P = 0.43$ , Table 3).

#### **Discussion**

##### **Nest Success vs. Nest Boxes versus Tree Cavities**

I found no evidence to support the hypothesis of nest boxes being inherently "safe" or more protected from nest predators than cavity nests. Nest predators were the most common cause of nest failure for Dual Crested Flycatchers in both nest boxes and tree cavities. Although nest boxes experienced higher nest predation in 1997, they were more vulnerable to egg predators in 1998. Nesting success in nest boxes decreased in

Table 2-1. Microhabitat metrics around nest boxes used for nesting by Green Crested Flycatchers over a 2-yr period.

Micohabitat variable	1997 ( <i>n</i> =11)	1998 ( <i>n</i> =11)
Covered-covered by leaves (%)	21(1) <sup>a</sup>	21(1)
Covered-covered by grass (%)	15(1)	14(1)
Covered-covered by shrubs (%)	19(1)	19(1)
Mean height (m)	1.3(0.1)	1.1(0.1)
Palustrine height (m)	0.8(0.0)	0.6(0.0)
No. of saplings (>1.5 cm dbh) per 0.4 ha	1.0(0.2)	2.4(0.9)
No. of small diameter trees (>1.5 cm dbh) per 0.4 ha	0.4(0.0)	0.4(0.0)
Total basal area (m <sup>2</sup> /ha)	22.1(2.2)	24.3(1.1)
Covered height (m)	19.3(0.4)	18.7(0.4)
Midstory height (m)	8.8(0.8)	10.7(0.5)

<sup>a</sup> Mean (SD).

only 10% or 100% because of a discrete increase in egg production during the incubation period (Table 2-2).

Direct evidence of predation by flying squirrels was available for the incubation period. Although direct evidence of flying squirrel predation was limited to 3 more circumstantial evidence (i.e., type of damage) to the nest suggests that flying squirrels may have been responsible for a substantial proportion of the total damage that occurred during the incubation period. Although others have speculated that flying squirrels are important predators on Great Crested Flycatcher nests (Layton 1997, White and Segarac 2000), this study is the first confirmed report of nest predation on the species by flying squirrels. Flying squirrels have been reported as predators of the eggs of other cavity nesting birds, including Black-capped Chickadees (*Poecile atricapillus*; Roth et al. 1994) and Red-cockaded Woodpeckers (*Picoides borealis*; R. Conner, pers. commun.; J. Kappeler, pers. commun.).

Wrens are generally found to prey on cavity nests during the nesting period and not during the incubation period (Endale 1994, Johnson 1996, MPE, Hendry and Smith 1998, Radford and Kenagy 1997). Taylor and Kadlecova (1991) reported two instances of predation by wrens on Great Crested Flycatcher nests, one on a nest containing 3 newly hatched nestlings and one on a nest containing 7 nestlings less than 1 week old. Similarly, in this study, direct evidence of nest predation by nest snakes was restricted to the nesting period. Together, these data strongly suggest that snakes were not primarily responsible for the high level of egg disappearance on nests during the second year of the study.

## Classes of Differential Pene Penetration in Pine Borer versus Pine Carpet

### Nest-site characteristics

Mean borer and carpet borer nests did not differ in height or in any nest-site variable that would influence nest construction, nor did these variables differ between years. Thus, borer and carpet borer nests cannot be attributed to a difference in the accessibility to tree trunks or of their sites to predators, either tree-dwelling ones or between years. This is perhaps not surprising given the relatively homogeneous structure of the pine plantations.

Physical dimensions of the nest roofs did not appear to be responsible for predation differences. Although I was unable to measure the size and shape of all tree crowns used by Great Crested Flycatchers (i.e., many were too large to fit completely), most rooves were old and had hybrid Woodpecker cavities, where openings ranged from 0.6 to 1.7 cm in diameter (unpubl. obs., Jenkins 1974; Stansfeld et al. 2000). Larger entrance holes have been found to offset aggression problems greater access to cavity nests (Diamond 1993a), but predation rates were highest at nest boxes, which had smaller entrances ( $\leq 1$  cm diameter) than most tree cavity nests. Obviously, temporal differences in pine predators (nest boxes were not affected by cavity nesters) and because all boxes had the same size entrance hole.

Diabetesacids birds are notorious for growing to older nest ages. Supporting evidence for the effect of antipredator traits on nest success is fragmental, with some studies finding antipredator traits and nestling mass to negatively correlate (Moller 1984, Rohwer et al. 1994; Geupel and Hupp 1997) while others finding no relationship (Hupp et

et al. 1994; Gould 1996; Givens et al. 1997). Regrettably, no previous study could account for the differences in nest success in nest boxes during the second year, because (1) nest boxes were thoroughly checked for nesting debris in the intervening winter, (2) the majority of nest boxes contained broken eggshells or signs of insect damage after predators.

**Birds by flying squirrels' nests and sites in cavities.** I measured whether the availability of nest boxes increased the density of flying squirrels. Any increase in squirrel densities would increase the risk of a squirrel opportunistically intruding and robbing a flycatcher nest. However, the numbers of flying squirrels among nest boxes did not change between years. Moreover, squirrels occupied the same number of nest boxes each year, indicating no increase in the movement of squirrels among nest boxes (Fig. 8). Squirrels not using nest boxes were not counted, but reported use of nest boxes was highly correlated with the total density of squirrels in study plots (because of the large number of boxes occupied by flying squirrels (Chapter 2)).

#### Possibilities for increasing fly nest predators

Several researchers have demonstrated a positive correlation between the risk of nest predation and the age of a nest site, both within (Wilson et al. 1991) and among (Miles and Li 1992; Miles 1995) cavity-nesting bird species, species and individuals that re-use nest boxes have lower rates of nest predation than non-reusers, but only at old nest sites for some time. One of the mechanisms behind this pattern is that nest predators may be more averse of the locations of older nest sites. Previous studies have shown that nest predation by mammals increases with the age of a nest box,

For example, Kishimoto and Suzuki (1997) identified two sources of Test Bias in the Myelinated Influenza test: bias decreased over time because of memory problems by seniors (Present bias) and confusion. These errors (Memory bias), which are important and common in elderly people from low socio-economic groups, represent memory for the location of test items used by Pineda-Gómez (Age-related memory) (Pineda-Gómez, 1999). In addition, new items for Cognitive Fluency (Language fluency) that were presented in a given year tended to be repeated in successive years (Dow and Peleg, 2002).

In this study, production of eggs decreased dramatically during the second year of the study. New items that were tested by Dual Coding Physicians were less likely to be recalled than old items being used for the first time. These results support the hypothesis that one problem in this study is related to explicit test items as a proxy measure, likely through the development of long-term spatial memory. It is unlikely that such storage development was the mechanism, given that only a small proportion of the available test items were repeated (see Materials and Methods, after Chapter 2).

However, problem areas in explicit tests placed in and from (after the conclusion of that study) were higher in test items that had been previously used by Dual Coding Physicians than in new items that had no previous memory storage (Engoff, 2002).

Using cognitive framework and theory (2000) discussed by Engoff, explicit and implicit memory is dependent. Word Recall (Myelinated materials) tends several days after the original problem event. Both observations suggest that a variety of test

predilection against flying like humans or probably going silent and returning periodically to them. Although flying squirrels were probably responsible for most predation on eggs in 1998, raccoons also may have played a role. Taylor and Kershner (1991) observed a small (11-mm) Inquiry at night taking a Great Crested Flycatcher nestling from a nest box two days after mother-feeding had disappeared from the same box; they speculated that the mother must return back to the nest because of her relatively small size.

### Summary and Conclusions

This study demonstrates that nest box use of songbirds varies year after year within. My results also underscore the importance of linking shifts in temporal dynamics of nest predators, to shifts in apparent food resources between natural areas and nest boxes over pre-moult/late breeding periods. If years were pooled in this study, then one would have concluded that Great Crested Flycatchers had declined nesting success in nest boxes and tree cavities. Worse yet, if one had drawn conclusions after only one year of study, then the conclusion would have been that Great Crested Flycatchers have enhanced nesting success when breeding in nest boxes. Many researchers fail to report temporal differences in nest boxes and nest predators in nest boxes (e.g., Espanola 1984, Nilsson 1984, Sauer and Alabama 1992, Purcell et al. 1999), which may weaken their conclusions about nest boxes. Other researchers present analyses that nest predators increase over time at nest boxes without discussing the statistical significance of the pattern (e.g., Delcourt et al. 1994, Dugger et al. 1999). When predators

unfortunately comparisons of breeding ecology in nest boxes versus free cavities, do not reveal the type repeat nest changes in these parameters.

Theoretical and empirical research indicates that nest predators may interact with the age of a nest box. The predation pressure because of nest boxes may actually make them more vulnerable over the long-term to nest predators than tree cavities (Hanson 1985a,b, 1989, 1993). Further research is needed to identify the factors – including type of predator (competition vs. raptor vs. avian), availability of alternative prey in the study area, percentage “use” of artificial nest cavities in the study area – that determine how nest predators will respond to nest boxes. For example, predation by avian nest pirates (Orell 1993) appears to be influenced by the abundance of alternative prey, at a study area with low rates of nest predation (7%) and abundant alternative insects. Korpitschka (1997) found little relationship between nest box age and predation rates by raptors. Researchers should take advantage of the opportunity to use nest boxes to study interactions of nest predators and their relevance to avian life history theory. I predict that, within a given area, nest predation rates in nest boxes will tend to be higher than those in tree cavities when the cavities are the same age (relatively short-lived (i.e., they didn't persist as long as the nest boxes)) and the nest predators in them are sufficiently robust to find eggs and nestlings or an unopened part of their strategi-ther-

To conclude other reproductive parameters obtained from nest box studies are not representative of birds nesting in tree cavities (Moller 1989) as to ignore the spatial and temporal variation that exists everywhere in nature. “Tree cavities” are not one state of a bird's existence. Cavity used by a given species are very considerably within a

study areas or sectors to map on their height, age, relative densities, structural integrity, availability to predators and to the threats to which they occur. These factors are multi-levels that allow the extrapolation of many of these factors to spatialised representations, thus facilitating the study of patterns, mechanisms or ecological relationships that otherwise would be difficult or nearly impossible to study (Koenig et al. 1991). The use of such factors in spatially disaggregated representations to study tree predation and its influence on treefall hazard theory should be encouraged rather than discounted.

## CHAPTER 4

### LIFE HISTORY TRADEOFFS IN CAVITY-NESTING BIRDS: WHY IS NESTING SUCCESS RELATED TO EXCAVATED-BEAN DENSITY (EXCAVATED BEANS PER HECTARE)?

#### Introduction

Cavity-nesting birds can be separated into two groups of species based on their nesting behavior: species that typically construct their own nest cavities (nestly) and those that do not (non-nestly), and species that do not construct their own nest cavities (i.e., non-nestly) and depend instead on natural holes or those created by excavators. Traditionally, studies that have compared species of nesting ecology from a life history perspective have grouped all cavity-nesting bird species into single nest-type (Lucas 1994; May 1997; Kikkawa 1999) or have focused only on non-nestlers and excluded their life history from initial cavity studies (Wilcox 1984, 1986). However, Li and Myers (1991) noted a rate of excavation and a rate of tree availability remaining in tree and open soil decreased after tree-excavation, suggesting higher nest failure than did excavators. Myers and Li (1991) suggested that life history traits may considerably influence excavators and non-excavators, with excavators generally having greater tree density, smaller clutch sizes, longer nesting periods, and fewer brood attempts per year.

In addition, Li and Moran (1999) found that non-matured (1) had at lower heights, (2) had greater tree associations, (3) had older root systems, and (4) tended to have smaller body size than matured. Li and Moran (1999) reasoned that each of these factors would afford tree predators increased access to the more unguarded citizen to non-adults (sexual difference in the tree), but these assumptions were not directly investigated. However, there was little variation in tree study, making it difficult to distinguish which factors were more important than others. For example, seeds that were larger were also more associated by understorey vegetation.

Predation pressure and other environmental conditions can vary among habitats. Non-adults can vary among different locations with different hunting techniques, different types of tree predators, as well as different cavity-hunting bird species. I report here the results of a study of cavity-nesting birds and other felid-hunting tools for a area of interest and a series of tree comparisons including (a) managed pine forests of the Redwood Creek Plateau. My objectives were (1) to confirm the proposed pattern of differential nest success and nest predation between mature and non-matured, and (2) examine the importance of environmental variables that have been suggested to discriminate differential nest success.

## Methods

### Study Site

I conducted my research at Camp Shasta Training Site in Shasta County, Northern California encompassing approximately 10,000 ha in the mountains of Shasta County, Shasta. My field assessments and I recorded 16 pairs of cavity-nesting birds as a

post-monsoon dominated by slash-paste [Forest Allotment] plantations (mean age, 10–40 years old) intermixed with longleaf pine [ $\geq 70$  years old] timber (unmanaged), with a significant component of >40 year-old trees). Most post-settlement was focused on native 3-ha plantation study plots, one 3-ha plantation study plot, and one 1.4-ha plantation with scattered patches of turkey oak (Quercus laevis; see Chapter 3 for a detailed description of plantations). Uncommon woody species were generally absent in native sites and usually limited to scattered turkey oak saplings or deer winter sites. Shrub, which rarely exceeded heights of 1.5–2.5 m (see Table 3-2), included non-palatable (greenwood gallberry, *Glycyrrhiza*, and other unpalatable species).

Potential seed predators of acorn-seedling. While the study area contained no snakes (likely spp. *Crotalus* (milk snake) flying squirrels (*Glaucomys sabrinus*) and other small mammals (e.g., *Peromyscus gossypinus*) were common, and several (Blue Jays, Crows—see Chapter 3—American Crows, Common Grackles).

#### Post-Searching and Monitoring:

My field assistants and I used standard field methods (Bartos and Geiger 1991) to search for acorn-seeds from mid-March through early July of 1990–1991. We noted near-peak acorn implantations among sites and did periodic (bi-monthly, bi-monthly) to maintain comparable search-effort among sites. I measured mean埋藏 depth in meters among three (Marin and Geiger 1993, Ralph et al. 1993). Sites located <10 m above ground were treated with a step-ladder and the canopy cleared with a light and tested source to determine acorn size and seed status. During 1990–1991, most acorns (>1 m high) in dead trees (young) were removed from the ground through

observations of adult behavior (e.g., carrying nest material or feeding the nestly; Marin and Ongpel 1995, Rajani et al. 1997, Mekhora et al. 1997), although some crevices in larger, more stable logs were associated with juvenile roosting tree-clinging behavior. In 1993, nest locations at the high were measured with a ruler mounted on a telescoping fiberglass pole (TreeTop II, Backyard Technologies, Inc., Monroe, California, USA). Eastern nests were measured approximately in 1991 while establishing study plots and these data also are included in analyses.

I did not actively search for nests of the Common Nighthawk (*Ptyonoprogne fuligula*) because it was a "back-and-forget" species to the study area, occurring in nests with predators (birds or possums) in brush piles, trees, and shrubs.

#### Differentiation of Hatch Year, Young Period, and Nest Success

I differentiated clutches into those that were assembled by hatching or by voice prior to first pre-hatching infestation (Marion 1973, Jenkins 1974, Shad 1982, Fitch et al. 1994, Taylor and Kershner 1995, Whittier et al. 1995) to estimate the length of the construction and nesting periods. At each species, I obtained inter-specific values for these parameters as I imagined nest patterns by hatching and by voice criteria.

The day the last egg in a clutch was laid was considered the final day of incubation for all species except for Eastern Screech-Owls (Oren 1994), which were treated as a one-by-one basis according to laying and incubation behavior. For species that I could not separate (i.e., some high nests from 1993–1997), I estimated the final day of incubation through observations of parental behavior at the nest (Marin and Ongpel 1995). I considered a nest to be successful if it produced ≥ 1 fledgling. Unattended markings re-

been felled if they were alive when checked) within 100 m of reported felling, and subsequent checks showed no evidence of predation or disturbance to the nest (Moen et al. 1997). Unpopped nest capsules typically contain 1–2 d after the reported date of felling in absence visual confirmation of the felling date.

I calculated daily survival rates for the incubation and nesting stages with the Mayfield method (Mayfield 1961, 1975) as modified by Hesler and Phausch (1993). Because daily survival rates for the two stages did not differ for any species (parametric survival Z test,  $Z^2 > 0.01$ , Appendix B, Hesler and Phausch 1993), I calculated a single daily survival rate for the entire nesting cycle and used that to determine overall nesting success for each species.

#### Nest site Selection

For each tree site, I recorded tree species and condition and measured nest height with a clinometer. I measured tree orientation at each nest in 1997 by estimating the percentage of the nest obscured by vegetation from a line drawn to the north, east, south, and west of the nest at nest height (Moen et al. 1997). Individual tree curves were generated for nests cavity-nesters throughout the course of the study and plotted for relationship between cavity size and tree success. When possible, cover distances were measured to assist in identifying the source (*i.e.*, tree cavity species) of cavities.

#### Statistical Analyses

I used chi-square analyses and logistic regression methods to assess COTRANLT (Hesler and Phausch 1993) in test for differences in daily survival probabilities

nesting species. I compared nest clutch size (by species) and non-significance with Mann-Whitney tests (MANNITAB; see 1990).

I determined the relationships among nest success rates, nest height, and body mass with Spearman's correlation coefficients; rank correlation coefficients were used because Chaffinches prevent it to assume that relationships between variables would be linear. Body mass covariates were obtained from Daan (1992). Within species, nest heights of successful and unsuccessful nests were compared with Mann-Whitney tests. In some cases, Red-bellied Woodpeckers made >2 nesting attempts at a given nest site within the same year; in these cases, I included only the outcome of the first nest in analyses of nest height covariate measures.

## Results

### Clutch Size and Nesting Physiology

I found a total of 119 nests of 11 cavity-nesting bird species (species lists are in Table 4-1). Clutch size was determined in 136 (11%) of these nests. Mean clutch size was lowest (1.0) for the Red-bellied Woodpecker and highest (1.9) for the Crested Chickadee and Dusky Crested Flycatcher (Table 4-1). Clutch size averaged across species was  $1.24 \pm 0.71$  (SE) for males and  $1.29 \pm 0.71$  for non-males (Mann-Whitney,  $P = 1.00$ ).

Double breeding was common for Red-bellied Woodpeckers and Dusky Woodpeckers, with Red-bellied Woodpeckers commonly laying their second clutch at the same cavity within the year. I could not obtain data for double breeding by any other species

Table 4.1. Mean (range) chick size, upper number of broods, and duration of incubation and nestling period for 11 species of cavity-nesting birds.

Species	Chick size	No. broods	Incubation (d)	Nestling (d)
<b>Barred Owl</b>				
<i>Strix varia</i>	3.6 (2.5)	1	13	21
<b>Belted Kingbird</b>				
<i>Tyrannus tyrannus</i>	3.3 (2.5)	1	13	21
<b>Brewer's Woodpecker</b>				
<i>Picoides dorsalis</i>	3.3 (2.5)	1	13	21
<b>Brown Creeper</b>				
<i>Troglodytes troglodytes</i>	3.3 (2.5)	1	13	21
<b>Brown-headed Nuthatch</b>				
<i>Sitta pusilla</i>	3.3 (2.5)	1	13	18
<b>Blue Grosbeak</b>				
<i>Guiraca caerulea</i>	3.3 (2.5)	1	13	21
<b>Carolina Chickadee</b>				
<i>Poecile carolinensis</i>	3.3 (2.5)	1	13	18
<b>House Wren</b>				
<i>Trochocercus australis</i>	3.3 (2.5)	1	13	21
<b>Red-eyed Vireo</b>				
<i>Vireo olivaceus</i>	3.3 (2.5)	1	13	21
<b>Red-shafted Flicker</b>				
<i>Colaptes cafer</i>	3.3 (2.5)	1	13	21
<b>Red-tailed Hawk</b>				
<i>Buteo jamaicensis</i>	3.3 (2.5)	1	13	21
<b>Spurred Towhee</b>				
<i>Zenaidura macroura</i>	3.3 (2.5)	1	13	21
<b>White-throated Swift</b>				
<i>Aerodramus spodiopygius</i>	3.3 (2.5)	1	13	21

\* Incomplete data.

although it is possible that the Tufted Titmouse successfully mixed two broods. On one occasion, I observed a Tufted Titmouse breaking a nest 150 m from an earlier successful nest, but Green-Crested Flycatcher occupied the nest before I could confirm if the same pair of parents was involved. The possibility also exists that some Red-tailed Hawks parents may have attempted to breed a third brood very late in the season, but nest searching and monitoring during August was outside the scope of this study.

#### **Nesting Success**

Mayfield estimates of nest success were generally higher for rarer than commoner species than for less commoner species, although there was considerable overlap between the two groups (Table 4-2). Mean nesting success ( $\pm$  SD) averaged across species with  $\geq 3$  nests was 67% (range 41–83%) for 5 rarer species and 68% (range 12–67%) for 4 more-common species (Table 4-2; Mann-Whitney,  $Z = 0.11$ ). Daily survival rates of observers did not differ from daily survival rates of rare observers ( $\chi^2 = 2.44$ , d.f. = 1,  $P = 0.12$ ).

Daily survival rates did not differ among observers ( $\chi^2 = 5.82$ , d.f. = 1,  $P = 0.21$ ) but differed significantly among observations ( $\chi^2 = 9.19$ , d.f. = 1,  $P = 0.002$ ). Because of the low nest survival rates of the Green-Crested Flycatcher and Eastern Phoebe relative to the Eastern Screech-Owl (Table 4-2), daily survival of Western Screech-Owl nests (0.91±1) was significantly greater than that of Green-Crested Flycatcher nests (0.58±1,  $P = 0.006$ ). Daily survival was not significantly greater for Eastern Screech-Owl nests than for Eastern Phoebe nests (0.93±1,  $P = 0.129$ ) because of the large variance measured with the Eastern Screech-Owl subsample.

Table 4-1. Number of successful nests out of total nests, number of days nests were observed, daily survival rates (RS) and Mayfield-style success estimates for 11 species of cavity-nesting birds, Geng Blending Training Site, 1995-1996.

Species	Observations				Mayfield nest success
	Successful	Total	days	Daily survival (RS)	
<b>Strigiformes</b>					
Red-Tailed Hawk	13	16	240	0.993 (0.991)	48.4
Downy Woodpecker	29	35	103	0.993 (0.994)	74.7
Harry Woodpecker	0	0	0	—	—
Northern Flicker	1	3	37	0.994 (0.915)	56.0
Carolina Chickadee	19	25	347	0.993 (0.994)	48.6
Brown Headed Nuthatch	11	16	268	0.993 (0.991)	62.1
<b>Passeriformes</b>					
Wood Duck	0	1	0	—	—
Eastern Kingbird	5	7	127	0.9913 (0.9962)	62.3
Green Crested Flycatcher	19	44	298	0.9947 (0.9989)	74.3
Tulip Tanager	11	14	159	0.9943 (0.9124)	49.6
Karri Blocket	1	4	47	0.9944 (0.9953)	71.5

Table 4-2. Causes of nest failure for eight cavity nesting species.

Species	Cause determined			Cause unknown <sup>a</sup>	Total
	Predation	Terror	Other <sup>b</sup>		
<b>Barred Owl</b>					
Red Bellied Woodpecker	7	2	6	13	38
Dowitch Woodpecker	3	0	0	3	6
Harry Woodpecker	0	0	0	1	1
Northern Flicker	1	0	0	0	1
Eastern Chickadee	7	2	1	1	11
Brown Headed Nuthatch	0	0	1	2	3
Total	33	6	8	28	58
<b>Non-passerines</b>					
West Duck	1	0	0	0	1
Eastern Screech Owl	1	1	0	0	2
Great Crested Flycatcher	18	1	0	6	25
Tulip Titmouse	3	1	0	0	3
Western Bluebird	0	0	1	1	1
Total	22	4	1	9	36

<sup>a</sup> Cause unknown could not be attributed to known cause of nest failure.

<sup>b</sup> Other natural causes of nest failure, including nest abandonment and disease.

### Cause of Nest Failure

Nest predators was the most common cause of nest failure (Table 4-1), occurring for 40 of 64 (62%) nest failures; 29% of all nest failures for which the cause was determined. Nest predators accounted for a larger proportion of nest failures among non-increasers than among decreasers ( $\chi^2 = 4.15$ , df = 1,  $P = 0.04$ ). Among non-increasers, 87% of all nest failures were attributed to nest predators.

Confounded nest predators included the same three (*Alopochen aegyptiaca*, yellow-rumped warbler (*Z. citrinella*), and northern flying-squirrel). Without removal of nests, I was unable to determine the relative importance of these predators. However, some unpaired observations can be made. Six males were observed pecking on nests (e.g. 2 Green Crested Flycatcher nests and 4 nest of 3 Red-bellied Woodpecker nests). These squatters were known to have preysed upon at least 2 Green Crested Flycatcher nests during the incubation period. In both instances, flying-squirrels or them and unpaired were observed on top of the bird nests <2 days after the presence was observed. One Common Chachalaca nest suffered extensive physical damage to the nesty wall possibly inflicted by a larger immature nest predator. In addition, 3 Downy Woodpecker nests were lost to other species of woodpeckers. A male Black Woodpecker stayed near Downy nests during the egg-laying period, and Red-bellied Woodpeckers depredated 3 Downy nests during the hatching period.

Failure from nest nests being suppressed because by wind and rain was more common for non-increasers than for non-decreasers (Table 4-1). Eight of 16 (50%) failed

secondary nests were lost from tree fall, whereas only one of the 34 (7%) failed nests of tree insurance was lost to tree damage (Fisher's exact,  $P = 0.877$ ).

### Nestling Behavior and Nestling Success

#### Species and condition of nestlings

Most nest sites were located in pine woods (Table 4-6). Nine trees were slash pine (40%), longleaf pine (21%), turkey oak (15%), and other pine species (15%). The Brown-headed Nuthatch, Carolina Chickadee, and House Wren nested mostly in pine trees and eastern live oaks. As a group, nest success rates tended to trend up with tree species, especially those that evergreen (Table 4-6), probably because of the availability of novel, hollowed, or live (and dead) oak holes.

#### Nest observations

Data collected from a sample of nests in 1977 indicated that nest occupancy was not a factor in the open forest species (Less than 1% of the cavity nests contained less than vegetation obscuring the nest). Thus, I discontinued measurement of nest success rates in unoccupied nests.

#### Nest length

Nest lengths of successful nests were significantly greater than nest lengths of unsuccessful nests for the Red-bellied Woodpecker, Eastern Screech Owl, and Downy Crested Flycatcher (Table 4-5). Nest lengths were not different for the Downy Woodpecker. Small samples in one or both of the nest outcome categories precluded running tailed statistical tests for most other species; for example, I had only 3 fail/nests of the Tufted Titmouse.

Table 4-4. Frequency (%) of tree associate types and tree species share the nest sites by cavity nesting birds (species with <1% total included). Percentages calculated separately for tree associates and for tree species.

Species	Tree condition			Tree species	
	Young	Dead portion of live tree	Live tree	Pine	Oak
<b>Associates</b>					
Red-bellied Woodpecker	99	1	0	41	59
Downy Woodpecker	91	3	0	33	66
Nuthatches	100	0	0	47	53
Carolina Chickadee <sup>a</sup>	100	0	0	91	9
Brown-headed Nuthatch	100	0	0	100	0
Average	99	1	0	47	53
<b>Non-associates</b>					
Eastern Screech Owl	100	0	0	50	50
Coast Crested Flycatcher	99	1	0	47	53
Tall-tailed Titmouse	47	51	0	40	60
Eastern Bluebird	100	0	0	100	0
Average	46	4	0	49	51

<sup>a</sup> Does not include three additional nests placed in bottom branch pairs.

Table 4. Median nest heights at successful and unsuccessful nests for 9 cavity-entering species, Camp Bluffing Tract, Costa Rica 1993-1999.

	Successful	Failed	<i>F</i> <sup>a</sup>
<b>Enterers:</b>			
Red-bellied Woodpecker	10.4 (29)	9.6 (26)	0.025
Downy Woodpecker	10.7 (17)	10.1 (14)	—
Marbled Plover	7.2 (3)	20.9 (1)	—
Chestnut Chlorodre	1.6 (14)	1.6 (11)	0.18
Brown-headed牛bird	3.6 (16)	4.9 (13)	0.75
<b>No enterers:</b>			
Spotted Towhee-Dad	2.8 (5)	1.7 (2)	0.00
Great Crested Flycatcher	7.3 (19)	3.9 (19)	0.00
Taiwan Titmouse	6.9 (12)	3.7 (9)	0.26
Eastern Kingbird	2.9 (3)	1.2 (3)	—

<sup>a</sup> One-tailed Mann-Whitney test of the hypothesis that Parent nest heights > Successful nest heights.

### Correlations among nesting success, nest height, and body mass

Comparing mate species, there was a positive correlation ( $r_s = 0.68$ ,  $P = 0.001$ ) between nest tree height and nest tree success (Table 4-1), and this relationship appeared to be linear (Fig. 4-1). Species with the lowest rates and heights (e.g., Chestnut Chukar, Eastern Phoebe) had lowest nest success. There were no other significant correlations among these variables (Table 4-1).

### Chestnut Chukar and eggs

Close monitoring of the chest in consecutive years allowed identification of the source of nest成功, and by cavity-nesting birds (Tables 4-7). Observations suggested there were two kinds, except for a sample of occasions in which large woodpeckers occupied the cavities of smaller non-polygynous species and enlarged them for their own use. Bush-tailed Woodpeckers provided most cavities for nest initiation from all very older non-mono species. A close relationship was apparently apparent between the Bush-tailed Woodpecker and the Chestnut Chukar (Table 4-7); of Bush-tailed Woodpecker cavities were still used in the second year and not used by the woodpeckers, then they usually were occupied by Chestnut Chukars. Chestnut Chukars cavities were used by several species, especially the Eastern Phoebe.

Bush-tailed Woodpeckers that used the same tree for a single year were less successful than Bush-tailed Woodpeckers that used it a newly excavated cavity, passing years, (but including second broods), 51 and 34 (77%) and attempted to do so, however, were substantially compared to 3 of 18 (17%) and although in 1-year-old nestlings (Student's *t*-test,  $P = 0.000$ ).

Table 4-6. Spearman's correlation coefficients between nesting success, nest height, and body mass of both species. Significant levels indicated in brackets.

	Nesting success	Nest height (m)	Belly mass (g)
Nesting success	—	0.600 (0.001)	0.624 (0.011)
Nest height	—	—	0.427 (0.044)
Belly mass	—	—	—

1. *Urgent medical intervention* (including resuscitation, stabilisation, or transfer to another hospital)

2. *Major surgery* (including major orthopaedic procedures, major gynaecological procedures, or major vascular procedures)

3. *Major trauma* (including major burns, major head injury, major limb fractures, or major abdominal or thoracic injuries)

ME	R	W	D	P	S	T	G	H	I	M	ED
1											None
2											None
3											None
4A											None
4B											None
5											None
6											None
7											None
8											None
9											None
10											None
11											None
12											None
13											None
14											None
15											None
16											None
17											None
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91											None
92											None
93											None
94											None
95											None
96											None
97											None
98											None
99											None
100											None

Gardenside

HHS

Health Sector Plan - Ontario Provincial Health Sector Plan, Ontario Ministry of Health and Long-Term Care, 1999-2000, 2000-2001, 2001-2002, 2002-2003, 2003-2004, 2004-2005, 2005-2006, 2006-2007, 2007-2008, 2008-2009, 2009-2010, 2010-2011, 2011-2012, 2012-2013, 2013-2014, 2014-2015, 2015-2016, 2016-2017, 2017-2018, 2018-2019, 2019-2020, 2020-2021, 2021-2022, 2022-2023, 2023-2024, 2024-2025, 2025-2026, 2026-2027, 2027-2028, 2028-2029, 2029-2030, 2030-2031, 2031-2032, 2032-2033, 2033-2034, 2034-2035, 2035-2036, 2036-2037, 2037-2038, 2038-2039, 2039-2040, 2040-2041, 2041-2042, 2042-2043, 2043-2044, 2044-2045, 2045-2046, 2046-2047, 2047-2048, 2048-2049, 2049-2050, 2050-2051, 2051-2052, 2052-2053, 2053-2054, 2054-2055, 2055-2056, 2056-2057, 2057-2058, 2058-2059, 2059-2060, 2060-2061, 2061-2062, 2062-2063, 2063-2064, 2064-2065, 2065-2066, 2066-2067, 2067-2068, 2068-2069, 2069-2070, 2070-2071, 2071-2072, 2072-2073, 2073-2074, 2074-2075, 2075-2076, 2076-2077, 2077-2078, 2078-2079, 2079-2080, 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20160-20161, 20161-20162, 20162-20163, 20163-20164, 20164-20165, 20165-20166, 20166-20167, 20167-20168, 20168-20169, 20169-20170, 20170-20171, 20171-20172, 20172-20173, 20173-20174, 20174-20175, 20175-20176, 20176-20177, 20177-20178, 20178-20179, 20179-20180, 20180-20181, 20181-20182, 20182-20183, 20183-20184, 20184-20185, 20185-20186, 20186-20187, 20187-20188, 20188-20189, 20189-20190, 20190-20191, 20191-20192, 20192-20193, 20193-20194, 20194-20195, 20195-20196, 20196-20197, 20197-20198, 20198-20199, 20199-20200, 20200-20201, 20201-20202, 20202-20203, 20203-20204, 20204-20205, 20205-20206, 20206-20207, 20207-20208, 20208-20209, 20209-20210, 20210-20211, 20211-20212, 20212-20213, 20213-20214, 20214-20215, 20215-20216, 20216-20217, 20217-20218, 20218-20219, 20219-20220, 20220-20221, 20221-20222, 20222-20223, 20223-20224, 20224-20225, 20225-20226, 20226-20227, 20227-20228, 20228-20229, 20229-20230, 20230-20231, 20231-20232, 20232-20233, 20233-20234, 20234-20235, 20235-20236, 20236-20237, 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20314-20315, 20315-20316, 20316-20317, 20317-20318, 20318-20319, 20319-20320, 20320-20321, 20321-20322, 20322-20323, 20323-20324, 20324-20325, 20325-20326, 20326-20327, 20327-20328, 20328-20329, 20329-20330, 20330-20331, 20331-20332, 20332-20333, 20333-20334, 20334-20335, 20335-20336, 20336-20337, 20337-20338, 20338-20339, 20339-20340, 20340-20341, 20341-20342, 20342-20343, 20343-20344, 20344-20345, 20345-20346, 20346-20347, 20347-20348, 20348-20349, 20349-20350, 20350-20351, 20351-20352, 20352-20353, 20353-20354, 20354-20355, 20355-20356, 20356-20357, 20357-20358, 20358-20359, 20359-20360, 20360-20361, 20361-20362, 20362-20363, 20363-20364, 20364-20365, 20365-20366, 20366-20367, 20367-20368, 20368-20369, 20369-20370, 20370-20371, 20371-20372, 20372-20373, 20373-20374, 20374-20375, 20375-20376, 20376-20377, 20377-20378, 20378-20379, 20379-20380, 20380-20381, 20381-20382, 20382-20383, 20383-20384, 20384-20385, 20385-20386, 20386-20387, 20387-20388, 20388-20389, 20389-20390, 20390-20391, 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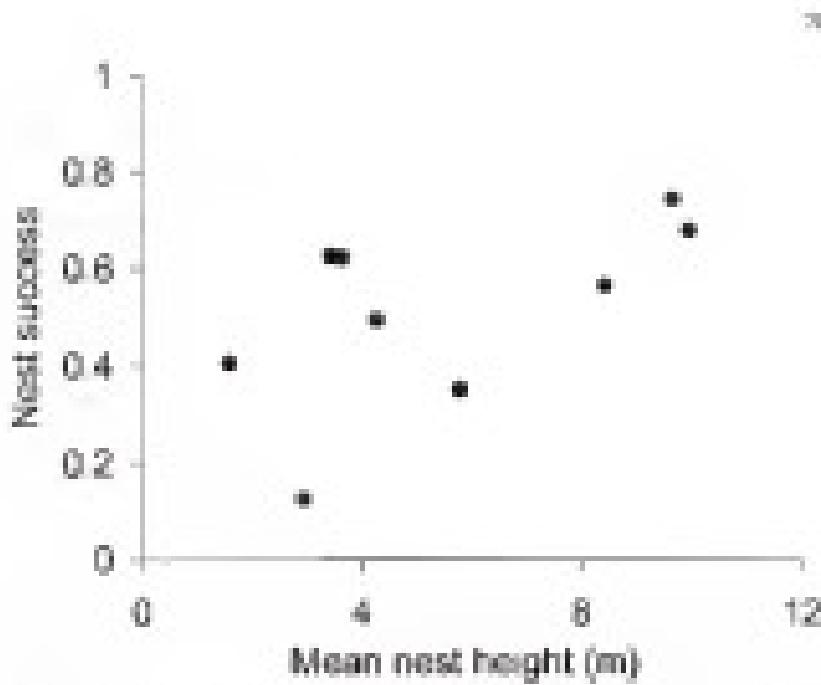


Figure 4.1 Relationship between mean nest height and nesting success rate (mean for 11 species of cavity-nesting birds, Camp Blanding Training Site, Florida, 1993–1994).

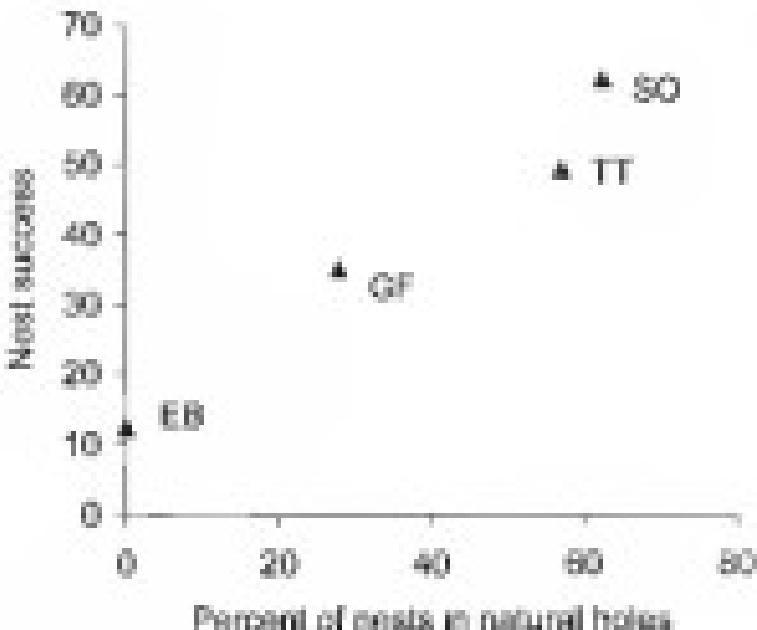


Figure 4.1 Relationship between percentage of nests built in natural holes & nest success rate for 4 species of tree-hole nester (EB = Eastern Bluebird, GF = Great-Crested Flycatcher, TT = Tufted Titmouse, SO = Tree Swallow (all data from Taita, 1995-1996).

Three non-endemic = the Eastern Screech-Owl, Chestnut Flycatcher and Tschudi Thrush = made relatively few of 'natural holes' (i.e., tree cavities not associated by other birds; Table 6.7). Natural holes excluded chickholes and hollow branches (i.e., trees the natural hollows opened between failed past years, and also perhaps limited by decaying stumps). I did not observe any of these natural holes being used for nesting in consecutive years. One of natural holes was previously occupied ( $n = 1$ %) with varying success rates for non-exemptor species, and this relationship appeared to be linear (Fig. 4.2).

### Discussion

#### Non-discrete Classification and Non-Exemption

Non-endemic generally had greater nest success than non-exempt, but the difference was not significant because of the large overlap between the two groups (Table 4.2). For example, the Eastern Screech-Owl, a non-exemptor, had greater nest success than ten exemptors: the Chestnut Flycatcher and the Northern Mockingbird were the only species that had success (Tschudi Thrush) but greater nest success than the exemptor (Chestnut Flycatcher).

This finding contrasts with the distinct differences between exempt and non-exemptors documented by Aronson et al. and Minton (1991) and Minton and Li (1992), the only other studies to compare nesting success of cavity-nesting guilds working in time and space. In their work, nest success was 0% or approaching 100% for several woodpecker species, and there was almost no overlap between the two guilds. Nest success for 11 exemptor species averaged 82% (range 43–100%) and for 8 non-exemptor

species treated (SP) (pages 21–26); Li and Martin (1991). Sample sizes of nests in their study were comparable to those in mine. Martin and Li (1992) had 110 nests for a third of the study, nesting species as those studied, and I had 17 nests for a third of the species in my study.

Nest success rates documented in my study area were usually lower than those reported from other locations for the most species (Li and Martin 1991; Johnson and Korman 1994; see Appendix C). For example, Mayfield nest success of the Crested Chickadee was lower in my study area (11%) than in Illinois (26%, Johnson 1992) and in my study in Tennessee (29%, Penn 1991). Nesting success for Eastern Bluebirds in my study area (33%) was lower than my study in the Northwest, my sample of nests was small, but even when nesting attempts as nest losses in the study area were excluded (n = 14 total nesting attempts), Mayfield nest success was still <30% (unpubl. data).

Nest predators appear to be higher in my study area than in many others (Appendix C). One possible explanation for relatively low nest success in Florida pine plantations is inter-specific differences in the density and diversity of nest predators. There is evidence in Florida to conclude that the density of nest predators is higher in southern pine barrens than in other plant communities in North America because it must reduce the chances of nest predators not finding nest sites (or low population densities measured). However, there are currently more species of snakes in the southeastern United States than in many other regions of the country, including high-elevation candleberry barrens in Arkansas (Babbitt and King 1979; Smith and Smith 1982). Two non-native species, the red snake (*C. coccinea*) and corn snake (*C. guttata*), are apparently important as predators on bird nests, including nests in tree cavities (e.g., Johnson 1992, 1994, 1995,

Layton 1993; Phillips and Dean 1991; also see Chapter 5). Moreover, evidence suggests that the Red-cockaded Woodpecker (*Picoides borealis*) evolved the behavior of drilling tree wells around its nest cavity as an adaptation to reduce predation by the cypress root weevils (Jenkins 1978; Randolph et al. 1996; McFarland 1992). But weevils are excellent climbers and spend most of their time above (R. Freudenthal, pers. comm.).

Thus, although this study confirmed that nest cavities have higher nest success than nest noncavities, the pattern was considerably weaker than that documented in high-elevation forest slopes in Arizona (Li and Marin 1991; Marin and Li 1992), where cavity nests represented lower levels of nest predation.

Additional research is needed to determine if high nest predation rates are typical of Florida pine forests. Within my study area, both loblolly Woodpecker nest success rates did not differ between young slash pine plantations and older longleaf pine woods (unpubl. data), indicating that high nest predation is not restricted to young pine plantations.

#### Evaluation of Overlapping Hypotheses About Differential Nest Success

##### Nest height

If predators prefer sites for higher nests, then successful nests should be higher than those that are unsuccessful. In this study, nest height and nest success were positively related across species. However, within individual species, successful nests were higher than failed nests for some species but not for others (Table 4-1). Thus, evidence for the nest-height hypothesis was mixed. Similarly, Li and Marin (1991) found a strong relationship between nest height and nest success when comparing more

value across species but did not find significant relationships within any species. Close examination of this pattern suggests that the range of nest heights used for nesting, together with the species' inherent predation pressure, determines whether successful nests are higher than failed nests for a given species.

An ecological consequence is that nest height usually affects territorial mammals, but this has yet to be demonstrated experimentally for specific territorial nest predators. However, a variety of evidence suggests that a threshold of vulnerability exists for many predators, with nests <2 m in height being most vulnerable to territorial mammals. For example, Alonso (1990) found that more declining nests ( $\approx 21\%$ ) at height were destroyed and the nesty walls damaged, predominantly by territorial mammals such as raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), and striped skunks (*Mephitis mephitis*). Similarly, Beckett and Robertson (1997) found degraded tree swallow (*Tachycineta bicolor*) nests averaged 1.1 m in height while successful nests averaged 4.5 m in height. Nilsson (1984) found that nests <2 m above ground were more likely to be preyed upon than higher nests for 3 species of cavity-nesters, but found no such relationship for 3 other cavity-nesting species, one of which suffered nest predators mostly from adjacent woodpeckers.

Many birds are likely to maximize a nest guild of anti-predators of varying body size and diverse foraging modes. Peltzer et al. (1990) argued that the short nests of Northern Cardinals (*Cardinalis cardinalis*) are subject to a nest guild of nest predators and high overall levels of predation, factors which combine to eliminate predictability with nest sites. They reported that this implies the lack of influence of nest-site variables such as height or orientation on the outcome of predicted nests (Casper et al. 1988). Peltzer et

et al. 1994). A variety of nest predator species was present in my study area, including tree-hole species that are excellent climbers. Predator species richness combined with high overall levels of nest predation may reduce the strength of selection for tall cavity nests in subtropical pine forests. Supporting evidence comes from the work of Sorenson (1999), who found that mean height of successful and unsuccessful nests did not differ for Red-bellied Woodpeckers or Downy Woodpeckers in two longleaf pine forests in western Florida.

It is also important to note that if the dominant nest predators in a given system are tall predators (e.g., owls, woodpeckers), then their nests would be taller than higher nests. The nest height hypothesis suggests that nest predators are predominantly terrestrial and have greater difficulty finding taller nesting higher nests than lower nests. There are aspects of this hypothesis that can be substantiated.

#### Nest orientation

The predictions of the nest orientation hypothesis were not supported by my data. The only nest site was partially obscured by branches of vegetation was those of the Crested Chickadee, an insectivore species with mean nest heights of 1.6 m.

Traditionally, choice of high nest sites by birds is thought to reduce predation by increasing the nest item diversity (e.g., Martin 1995), presumably by visually oriented nest predators. Increased foliage density may reduce the risk of nest discovery by obscuring the nest (Soler 1976, Murphy 1981, Wittenmark and Dunc 1985), inhibiting the movement of predators (Rosenzweig and Raine 1988) or increasing the number of possible sites that a predator can inspect (Martin and Kaper 1988). The idea that dense foliage would have the opposite effect on cavity nests (i.e., increased nest predation) appears to have been developed by Bellairs-Taylor and Pooten (1986) who found more

When made unoccupied by open-savag visitors had lower nest predation than nests surrounded by dense vegetation. They speculated that dense vegetation could allow competitors (e.g., songbirds) to nest closer to the nest than would be the case if they did not have the resources. Although their work has been cited by others (e.g., Pach-Hall, Li and Martin 1991) as evidence that predators have wider accounts cavity nests when they are occupied, this phenomenon has yet to be documented. Moreover, if concentration of the nest by vegetation is beneficial for open-savag visitors but not for cavity-nesters, then it follows that nest predators must use different cues to find open-savag and cavity nests, a concept for which there is also no evidence.

I found no evidence that Cuckoo Whoopees destroyed or usurped nests from others, contrary to the prediction by Gossel et. al. (1992) that competition from others would be a major source of nest failure for secondary cavity-nesting birds in pine plantations. In fact, Cuckoo Whoopees rarely used tree cavities or nest sites owned/preserved by other birds, mice, moths and arthropods or brush piles and palmetto bunches.

#### Nest quality: age

Nest predators and the age of the nest site were positively correlated, both across and within cavity-nesting bird species. Nest survival species that made use of natural holes had greater nest success than those that used man-made structures (Gossel, Loukny and Albrecht 1992). I found that nest predators in the Pied Flycatcher (*P. flycathetus*) population were significantly higher in old nest-palmar variation than in natural hollows (unpublished data by Joseph Bell and Avery). These holes were abandoned

in their study area, thus such woodpecker holes would have had less previous nesting activity than such woodpecker holes, which, by definition, had always had previous bird use.

Among Red-bellied Woodpeckers, birds that reused their nest cavities in successive years had lower nest success than those that reutilized prior cavities each spring. Nilsson et al. (1991) found the same pattern for Black Woodpeckers (*Dendrocopos leucotos*) too. Among Great Crested Flycatchers, birds using older nest holes suffered higher nest predation than those using new nest holes (see Chapter 14, which constitutes further support for the hypothesis that nest age is correlated with predation risk). In summary, I found a variety of evidence that nest cavities have inherently low nest success because nest predators learn over time by exploring older nest sites as a prey resource.

#### Body size

Body size was not correlated with nest success in this study. Predictions made on cavity-nesters were generally correlated with the species' body size (Dunn 1977, L. and Martin 1991) but Nilsson (1991) found the opposite result. In addition to body size, other factors [e.g., aggression, mobbing behavior, vigilance] probably influence a species' effectiveness at deterring or repelling nest predators.

#### Conclusion

Cavity-nesting birds had lower nest success in the young, regenerated pine forests of southeast Florida than in older forests in North America. Although nest cavities had greater nest success than peer non-cavities, the pattern was not so clear

as as the predation-prone ( $F^*$ , *predator*). Results similar to Li and Minns (1991) upon which much bat-hunting theory about cavity nesting bats has been based (Minns and Li 1993). High levels of nest predation combined with the relatively few targets of cavity nests in a young, inexperienced flock may have measured the difference between the two nest types in my study.

This study provides additional evidence for the importance of cavity size (a primary covariate) and nest height as factors determining differences in bat-hunting rates of cavity-nesting bats. Because these two factors frequently step by correlated, manipulative experiments to simultaneously address these factors would provide further insight into the relative importance and how they might interact in different situations.

Nevertheless, the tight relationship between nest rates of the Red-tailed Woodpecker and Great Crested Flycatcher provides strong support for the hypothesis that cavity size may be of primary importance in determining lower nest success and consequently higher annual reproductive effort (Minns and Li 1992) in nest-excavators. Close monitoring of individual cavities over a 3-yr period indicated that nest-excavators will excavate new holes as soon as they were vacated. Great Crested Flycatchers were highly dependent on the cavities excavated by Red-tailed Woodpeckers (Table 4-7); I even observed a few instances where Red-tailed Woodpeckers and Great Crested Flycatchers used the same nest cavity sequentially within the same season. Predation risk increased in successive years within a given nest site, even though nest location and nest height apparently did not change over time.

My results also underscore the importance of looking at local and regional differences in nest predation. In most studies, the identity of nest predators is unknown

(e.g., classification of tree predators from nest counts or with suitable techniques (Larivière 1994) and a variety of tree predators may respond differently to tree height. More research is especially needed on the ecology of tree-climbing vertebrates—systems still known.

Although it may be appealing to focus on vertebrate interactions (i.e., with predators) to explain nest-site selection of forest birds, it is equally important to recognize the importance of vertebrate interactions at a community of cavity-nesting birds (i.e., inter-specific competition for nest cavities; associations between nest cavities and occupancy). A simple explanation for the greater vulnerability of nest-sites to nest predators is that non-predators seek to reuse opportunities. In their studies of nest sites, particularly if they are used in bad or unsuitable circumstances, birds can be the first to disappear, leaving fewer cavities available. Under this scenario, nest predators need necessarily a selective force, because nest-site selection is determined only by the pattern of age and density in the cavity reservoir and the interspecificly variable resources based on body size and food-dominance. Wilson (1984) found that smaller cavity-nesting birds were forced to nest lower on the presence of older species. As a consequence, non-predators are forced to accept the cavities that are available, involving old and unsuitable cavities that have an increased risk of nest predators.

## CHAPTER 3 CONCLUSIONS AND FURTHERS

### Synopsis

New-arrivals are likely to be rare and located in the young part of the forest during the Breckland Forest Phase, because tree density is positively correlated with tree density, tree age, and the abundance of herbivore species (see below et al. 1992; Wilcox et al. 1990). However, habitat quality may set an upper limit to the availability of a given area for breeding trials. For example, the densely packed rich grass plantations I studied appeared to be marginally suitable as breeding habitat for Eastern Bluebirds (Table 6a), that, persisting populations increase regardless of the number of territories that become available. Most sites of many cavity-entering species, including Eastern Bluebirds and Great Crested Flycatchers, are characterized by associations with young stages tree density of trees, and a mature open canopy (soybean data, Miller 2000), all features that were rare in these pristine study plots.

I found that new-arriver species that were sited in cavities or nests were most likely to be rare rare (Table 1), whereas those that were approximately at their natural centers and common (e.g., Carolina Wren, *Zenaidura macroura*) were not easily located (Chapter 2; Brown and Rohr 1980). Use of a variety of cavity types also was

coordinated with tree species for a given species, probably because there were too few presence/absence nesting birds (Chapter 4).

Martinez-Li et al. (1992) suggested that spatial and temporal variability in the quantity and quality of nest sites could have increased reproductive effort by nest initiators (e.g., larger clutch sizes, more food storage per pair/m<sup>2</sup>) in nonbreeding contexts. However, contrary to Martinez-Li et al. (1992), I found no significant difference in clutch size or daily nest survival rates between nesters and non-nesters (Chapter 4). Clearly, site-specific factors are also of play, and these link history relationships merit further exploration.

Nest predators were on average twice more likely in my study area than the same species to eat brood (see Appendix C). I found a variety of evidence supporting the importance of cavity size as a determinant of nest success. Species that are able to use a variety of nest sites had greater nest success than those that relied predominantly on old woodpecker cavities that had been used by birds in the previous year. Egg depredation rates increased by the Dusky Crested Flycatcher (*Muscicapa dauurica*) increased during the second year and these were available evidence presented in Chapter 4 indicated that was likely a result of nest predators learning the location of nest boxes or developing search images for them.

Finally, prescribed burning treated to facilitate the recovery and use of nest trees by secondary cavity-nesters in this study. From a management perspective, if decreasing cavity-nesting bird populations is a management goal in fire-maintained pine

forest, managers may find that the addition of new trees to already forested areas will result in the highest local benefit of cavity-making tools.

### Research Needs

Community-level studies of avian nest success have become common in many regions of the United States during the last 5–10 years, providing insight on the effects of timber management practices, habitat fragmentation, and landscape changes on populations of both open-woodland and cavity-nesters, and breeding migrant species and resident species. However, the type of information is still unknown in Florida, a state that already has less than 10% of its original coverage of longleaf pine (Paine 1989). Research on nest and success of the longleaf pine avifauna has been conducted on two bird species—the Bachman's sparrow (*Passerina cyanea*) and Northern bobwhite (*Turkey megalura*). My study is the first to measure nest-situation and nesting success of a community of cavity-making tools in southern pine plantations. It is difficult to fully interpret my findings because of the lack of similar information elsewhere, but unmanaged pine forests in the Southeast. Comparative studies of avian reproductive success in different forest types and landscapes should be a priority for future research in Florida. Future research in Florida should focus on nest-site selection, nest predators, and nest parasites—topics that are still almost completely unexplored in savanna landscapes in Florida.

Pine plantations have been uniformly studied, especially in southern pine forests. From a management perspective, additional research is needed on how nest predators are

affected by site characteristics. Potters and the need for further research on the ecology of the redpoll flying appear as a main site component and nest predictor, both between plantations and in longleaf pine forests and scrublands. Present studies have advanced, but generally ineffective, results from experiment designs designed to assess the impact of flying squirrels on cavity nests (Casper and Ryckliffe 1991; Casper et al. 1994; Mitchell et al. 1997).

A new critique also need a better understanding of the way that different nest predator species are to locate cavity nests. Although I found support for the concept that higher nests are less conspicuous and/or less vulnerable to nest predators (Chapter 4) and for the concept that cavity trees positively correlated with predators risk (Diagram 14), carefully designed manipulative experiments are needed. These outcome variables are usually inter-correlated (Li and Moore 1997), and thus, they form a set of overlapping hypotheses that can best addressed with factorial experiments (Quinn and Deeks 1997). Nest boxes are likely to be an associated tool for testing some of these relationships between nest predators and nest-site selection by cavity nesting birds.

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APPENDIX A

RELATIVE ABUNDANCE OF BIRDS IN SLASH PINE PLANTATIONS  
CAMP BLANDING TRAINING SITE, FLORIDA, 1991-1992

**Appendix A.** Relative abundance of birds at each year group status, Camp Blanding Training Site, Florida, 1990-1997. Birds were surveyed in 73 permanent permanent stations from January 1990 through April 1997 (n = total bird group count made). The two most abundant species are in boldface.

Common name	Scientific name	Total Counts <sup>a</sup>		Frequency <sup>b</sup>
		Number (%)	Rate	
Screech-owl	<i>Megascops asio</i>	1 (0.1)	0.00	
Belted Kingbird	<i>Tyrannus tyrannus</i>	1 (0.1)	0.01	
Wild Turkey	<i>Meleagris gallopavo</i>	4 (0.1)	0.02	
Northern Bobwhite	<i>Colinus virginianus</i>	1 (0.1)	0.04	
Hunting Dove	<i>Zenaidura macroura</i>	9 (1)	0.02	
Yellow-bellied Cuckoo	<i>Coccyzus americanus</i>	9 (0)	0.00	
Eastern Screech Owl	<i>Otus asio</i>	9 (0)	0.00	
Giant Horned Owl	<i>Bubo virginianus</i>	0 (0)	0.00	
Raven Owl	<i>Bubo virginianus</i>	0 (0)	0.00	
Common Nighthawk	<i>Chordeiles acutipennis</i>	1 (0.1)	0.01	
Check-willed Flycatcher	<i>Crypteliger variegatus</i>	7 (0.1)	0.01	
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	62 (4)	0.46	
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	9 (0)	0.00	
Downy Woodpecker	<i>Picoides pubescens</i>	56 (3)	0.16	
Red-cockaded Woodpecker	<i>Picoides borealis</i>	2 (0.1)	0.00	
Northern Flicker	<i>Colaptes auratus</i>	1 (0.1)	0.01	
Pileated Woodpecker	<i>Dryocopus pileatus</i>	6 (0.1)	0.02	
Woodpecker sp.	...	0 (0)	0.00	

## Appendix A. Continued.

Common name	Scientific name	Total Count Number (%)	Frigidity Rate
Eastern Wood Pewee	Cyanoptila ruficeps	1 (1)	<0.01
Great Crested Flycatcher	Muscicapa cristata	17 (48)	<0.01
White-eyed Vireo	Vireo griseus	18 (52)	<0.01
Yellow-throated Vireo	Vireo flavifrons	3 (10)	<0.01
Red-eyed Vireo	Vireo olivaceus	1 (3)	<0.01
Blue Jay	Cyanocitta cristata	14 (42)	0.13
American Crow	Corvus brachyrhynchos	13 (31)	0.19
Fish Crow	Corvus neoponensis	9 (21)	<0.01
Cowbird	Corvus sp.	9 (21)	<0.01
Common Grackle	Pooecetes gramineus	36 (9)	0.08
Tulip Tanager	Flamboyia tulipa	39 (10)	0.08
Brown-headed牛背鶲	Sturnus pusillus	15 (4)	0.08
Carolina Wren	Thryothorus ludovicianus	79 (20)	0.08
Kiss-gape Gnatcatcher	Polioptila caerulea	23 (6)	0.08
Eastern Bluebird	Sialia sialis	4 (1)	0.08
Wood Thrush	Hylocichla mustelina	9 (19)	<0.01
Gray Catbird <sup>1</sup>	Dumetella carolinensis	9 (1)	0.01
Brown Thrasher	Toxostoma redivivum	1 (3)	0.03
Northern Flicker	Colaptes auratus	9 (2)	0.02

## Appendix A. Continued

Common name	Scientific name	Total Counts Number (%)	Frequency (%)
Pileated Woodpecker	<i>Dryocopus pileatus</i>	559 (36)	8.81
Common Yellowthroat	<i>Erythrocercus livingstonei</i>	19 (1)	0.38
House Wren	<i>Troglodytes aedon</i>	8 (0)	0.00
Summer Tanager	<i>Piranga rubra</i>	18 (1)	0.32
Eastern Towhee	<i>Pipilo erythrurus</i>	154 (9)	9.48
Red-tailed Sparrow	<i>Zenaidura macroura</i>	9 (0)	0.00
Northern Cardinal	<i>Cardinalis cardinalis</i>	98 (6)	9.81
Brown-headed Cowbird	<i>Molothrus ater</i>	19 (1)	0.32
Total <sup>a</sup>		1,907	

<sup>a</sup> Total number of birds counted within 3 km radius of the observer.

<sup>b</sup> Proportion of total prior count weeks during which the species was recorded at any distance from the observer.

<sup>c</sup> Unusual breeding status, potential breeder but very few birds seen after April.

<sup>d</sup> Data does not include waterfowl; mammals recorded occasionally or not at all: Baby-faced Nighthawk (*Chordeiles acutipennis*), Cedar Waxwing (*Cathartes aura*), Northern Mockingbird (*Mimus polyglottos*), Black-throated Blue Warbler (*Dendroica caerulescens*), Yellow-rumped Warbler (*D. coronata*), Palm Warbler (*D. palmarum*), American Goldfinch (*Carduelis tristis*).

APPENDIX II

MULTIPLIED DAILY SURVIVAL RATES OF CAVITY-NESTING BIRDS  
AT EACH STAGE OF THE BREEDING CYCLE

Appendix B. Differences (Classical Z scores) in Mayfield study survival rates (%) of each stage of the nesting cycle (Cape Breton Trapping Site; Thesis, 1983-1984).

Species	No. nests	Daily survival rate (%)			$Z^*$
		Inbreeding period	Nesting period	?	
<b>Exoscopers</b>					
Red Bellied Woodpecker	18	0.9999 (0.0000)	0.9997 (0.0000)	1.000	
Downy Woodpecker	25	0.9950 (0.0050)	0.9997 (0.0044)	0.710	
Hairy Woodpecker	1		0	0	-
Northern Flicker	3	1.0000 (0.0000)	0.9992 (0.0004)	0.010	
Carolina Chickadee	25	0.9924 (0.0024)	0.9923 (0.0023)	-0.001	
Brown-headed Nuthatch	14	0.9947 (0.0077)	0.9923 (0.0077)	-0.367	
<b>Non-exoscopers</b>					
Wood Duck	1		0	0	-
Eastern Screech-Owl	7	0.9973 (0.0027)	0.9952 (0.0047)	-0.403	
Least Crested Flycatcher	44	0.9943 (0.0048)	0.9935 (0.0058)	-0.100	
Titled Titmouse	18	1.0000 (0.0000)	0.9977 (0.0123)	1.761*	
Tufted Titmouse	6	0.9944 (0.0044)	1.0000 (0.0000)	-1.107	

\*  $\alpha/2 = P = 0.05$ .

#### APPENDIX C

LITERATURE REVIEW OF DATA ON MINERAL SUCCESSIONS OF  
CAVITY BRETTING ROCK SPACES THAT OCCUR IN THE STUDY AREA.



## Appendix C: Current

Species	Year	Location	Min %	Max %	% habitat area within watershed	% watershed area within watershed	Notes
Lake Stinkpot	PL	Rocky shoreline	0	10	0-38 <sup>a</sup>	0-38	Water Quality
PL	Shallow marshy areas	0	20	0-20 <sup>b</sup>	0-20 <sup>b</sup>	Water and Waterbody Health	
PL	-	-	0	10	0-10 <sup>b</sup>	0-10 <sup>b</sup>	Water and Waterbody Health
GD	Shallow marshy areas	0	20	0-20 <sup>b</sup>	0-20 <sup>b</sup>	Water and Waterbody Health	
GD	-	-	0	10	0-10 <sup>b</sup>	0-10 <sup>b</sup>	Water and Waterbody Health
GD	Shallow marshy areas	0	20	0-20 <sup>b</sup>	0-20 <sup>b</sup>	Water and Waterbody Health	
GD	-	-	0	10	0-10 <sup>b</sup>	0-10 <sup>b</sup>	Water and Waterbody Health
GD	Shallow marshy areas	0	20	0-20 <sup>b</sup>	0-20 <sup>b</sup>	Water and Waterbody Health	
GD	-	-	0	10	0-10 <sup>b</sup>	0-10 <sup>b</sup>	Water and Waterbody Health

<sup>a</sup> Waterbody Health.

<sup>b</sup> Waterbody Health or Waterbody Health and Water Quality.

<sup>c</sup> Waterbody Health or Waterbody Health and Water Quality.

<sup>d</sup> Waterbody Health or Waterbody Health and Water Quality.

<sup>e</sup> Waterbody Health or Waterbody Health and Water Quality.

#### Biographical Sketch

Karl E. Miller was born and raised in Baltimore, Maryland. He attended Community College in North Carolina, where he received a B. A. in 1981, with a concentration in Biology, in 1984. Karl then worked for 8 years as a seasonal employee for the National Park Service and US Forest Service in a variety of environmental assessment and natural resource management positions. After studying at the School for Field Studies research station in south Queensland, Australia, in 1991, he decided to pursue graduate education. Karl was admitted to the University of Florida in 1993 and graduated with a Master of Science degree in wildlife ecology in December 1997.

Karl graduated from the University of Florida with his doctorate in December 2000. He has conducted research on interesting projects on rufous-necked woodpeckers, American kestrels, Blue Gulls, and Black-bellied Plovers. Although primarily an avian ecologist, Karl also has conducted research on white-tailed deer and Florida manatees.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Robert P. Morrison  
Associate Professor of Wildlife Biology and  
Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Douglas J. Lovett  
Associate Professor of Wildlife Biology and  
Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Robert H. Rappaport  
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Stephen R. Pauchant  
Professor of Wildlife Biology and  
Conservation

The dissertation was submitted to the Graduate Faculty of the College of Agricultural and Life Sciences and to the Graduate School and was accepted to partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December 2000

  
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